

A REVISION OF THE GENUS *PHENACOHELIX* SUTER, 1892 (MOLLUSCA: PULMONATA) WITH DESCRIPTIONS OF FOUR NEW SPECIES AND REASSIGNMENT OF *THALASSOHELIX ZICZAG* (GOULD, 1846)

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Abstract. Four new species in the genus *Phenacohelix* Suter, 1892 are described from New Zealand: *P. aurea* from Auckland north, *P. brooki* from a limited area in the north-east of the North Island, *P. hakarimata* from the middle of the North Island, and *P. mahlfeldae* from Otago, Southland and Stewart Island. *Thalassohelix ziczag* (Gould, 1846), from the northern half of the North Island, is transferred to the genus *Phenacohelix*. *P. ponsonbyi* (Suter, 1892) is redescribed, and details of anatomy are supplied for *P. giveni* (Cumber, 1961), *P. lucetta* (Hutton, 1884), *P. perplexa* (Murdoch, 1897), *P. tholoides* (Suter, 1907) and the type species *P. pilula* (Reeve, 1852).

KEYWORDS: *Phenacohelix*; *Thalassohelix*; *P. aurea* n. sp.; *P. brooki* n. sp.; *P. giveni*; *P. hakarimata* n. sp.; *P. lucetta*; *P. mahlfeldae* n. sp.; *P. perplexa*; *P. pilula*; *P. ponsonbyi*; *P. tholoides*; *P. ziczag*.

INTRODUCTION

In the most recent revision of *Phenacohelix* Suter, 1892, Cumber (1961) divided the genus into two sub-genera, *Phenacohelix* s. str. for *P. ponsonbyi* (Suter, 1897), *P. pilula* (Reeve, 1852) and *P. subantarctica* Suter, 1909, and *Neophenacohelix* Cumber for *Phenacohelix* (*Neophenacohelix*) *giveni* Cumber, 1961, *P. (N.) tholoides* (Suter, 1907), *P. (N.) perplexa* (Murdoch, 1897) and *P. (N.) stokesi* (Smith, 1884). While Cumber's work was evidently thorough, with taxon diagnoses on shell and radular characters, and information provided on distribution, shell variation and ecology, *P. subantarctica* was subsequently transferred to the punctid genus *Laoma* by Climo (1969). Furthermore, Powell (1979) did not adopt Cumber's subgeneric classification of *Phenacohelix*. Powell (1979) recognised that *P. (N.) stokesi* was synonymous with *P. lucetta* (Hutton, 1884), the latter having priority.

In this paper I revisit all previously described species of *Phenacohelix* from the viewpoint of anatomy, and describe four new species on the basis of conchological and anatomical characters. Further, I describe the anatomy of *Thalassohelix ziczag* (Gould, 1846) and, on the basis of conchological and anatomical characters, transfer this taxon to the genus *Phenacohelix*. Powell (1979) had noted the uncertain status of the genus *Thalassohelix* Pilsbry, 1892 and that *T. ziczag* has no great shell similarity with the type species *Thalassohelix zelandiae* (Gray, 1843). This and my earlier studies (Goulstone 1995, 1996) clearly point to anatomical investigation providing for different interpretations of affinities than that arrived at by studies of shells or radula alone, which has been the more traditional approach. In this present study, I have retained

for the sake of nomenclatural stability all examined species within *Phenacohelix* though anatomical details suggest possible domicile elsewhere. Their proper assignment to genera must await improved understanding of the anatomy of the New Zealand Charopidae.

METHODS

The taxon descriptions and distributions given in this paper are based mainly on specimens held in the Auckland Museum. Accession numbers preceded by "AK" indicate specimen material used in anatomical studies and/or referred to in developing the taxon descriptions. Accessions designated by "AK-L" signify specimens examined during the present study but held in the collections as bulk site samples. For *P. lucetta* and *P. perplexa* I have not listed "Other material examined" as the data presented by Cumber adequately depicts the distribution of these taxa as indicated by the material in the Auckland Museum collections. In the case of *P. ziczag*, *P. pilula* and *P. giveni*, the Auckland Museum holdings are too large to contemplate listing all locality data (for *P. giveni*, for example, there were at the time of preparing this manuscript, some 900 registered accessions). Selected, additional material was examined from Museum of New Zealand Te Papa Tongarewa (formerly National Museum of New Zealand), Wellington (accessions designated by MONZ). All collection dates are for the 20th century, and all geographic position co-ordinates for localities refer to eastings and northings in the NZMS 260 map series.

The dimensions of the shells were determined by callipers. The height measurements for shells with preserved animals are usually approximations as the partially retracted animals often partially obscured the shell aperture. Tables of shell measurements of most of the specimens dissected are supplied in "Remarks". Shell colours were determined by placing the dry specimens under the microscope on Munsell's Soil Colour Charts (1994). In the taxon descriptions, shell colours are given for fresh shell specimens, with the colour first defined in words and then by the chart (e.g., 5YR) and swatch (e.g. 8/2) numbers. Animals preserved in alcohol or formalin were dissected under a stereomicroscope. Tissues from dissected animal have been retained in the Auckland Museum collections, often with the fragments of shell from which the animal had been extracted.

SYSTEMATICS

Family CHAROPIDAE Hutton, 1884

Subfamily AMPHIDOXINAE Albers, 1850

Genus *PHENACOHELIX* Suter, 1892

Phenacohelix Suter, 1892. Transactions of the New Zealand Institute 24: 270. Type species, by subsequent designation, *Helix pilula* Reeve, 1852.

Neophenacohelix Cumber, 1961. Transactions of the Royal Society of New Zealand 1: 164. Type species, by original designation, *Phenacohelix* (*Neophenacohelix*) *giveni* Cumber, 1961.

REMARKS

Suter (1892) designated *P. ponsonbyi* Suter, 1892 as the type species of *Phenacohelix*, which is represented in the two main islands of New Zealand. However, Powell (1979) showed that the type should more properly have been *Helix pilula* Reeve, 1852. The type specimen of *H. pilula* in The Natural History Museum, London, as discussed by Cumber (1961), is in poor condition and only bears the locality designation "New Zealand". Photographs of this type specimen,

held by the Museum of New Zealand, show that it is conchologically identical with the material treated in the present paper as *Phenacohelix pilula* (Reeve) and for which I have supplied a description of the anatomy.

The anatomical information provided by Solem (1978) for *Phenacohelix pilula*, based on specimens obtained by Laurie Price from Kaitaia, actually relates to *Phenacohelix aurea* n. sp. (see below) and, with the type concept in mind, cannot therefore be taken as indicative of the anatomical features of the genus *Phenacohelix*.

Phenacohelix aurea n. sp.

Figs 1, 12

Phenacohelix pilula: Solem, 1982: 62. Not *Helix pilula* Reeve, 1852 = *Phenacohelix pilula* (Reeve, 1852).

ETYMOLOGY

From *aurea*, Latin, golden.

DESCRIPTION

Shell

Small, globose, narrowly perforate, with umbilicus partly closed by reflected columella, sutures moderately deep. The type shell, from an adult specimen, is c. 3.3 mm high by 2.9 mm wide, five and a quarter whorls, final whorl 0.2 of total shell diameter. Protoconch of one whorl, 0.15 of total shell diameter in the type, with c. 12 spiral striations. Teleoconch whorls have strong primary axial ribs, sharp at their apex, with crowded fine secondary axials along their bases and in the interstices. First teleoconch whorl with 30 primary axials, the last whorl with 50 primary axials. Axials emerging at right angles from the sutures, but soon curving slightly (at the shoulder) to mirror the shape of the peristome at which accretionary shell growth occurs. On ventral surface these axials are sinuous and terminate in the umbilicus. Teleoconch whorls have crowded microscopic spiral striations, more obvious in the umbilicus and at the suture, but not apparent at the apex of the primary axials. Colour uniformly brown 7.5YR/5/4 when fresh, but shells from dead animals fade quickly to very pale brown 10YR/8/3. Table 1 gives shell measurements for this species.

External Morphology

Mainly white. Caudal horn prominent on foot posterior with pedal groove ending in a deep caudal foss. Margins of the foot sole not much crenellated.

Reproductive Anatomy

Ovotestis comprising two primary clusters of alveoli, embedded in digestive gland close to stomach apex; proximal cluster (about 0.8 mm wide) larger than distal cluster (0.5 mm wide). Ovotestis feeds into the hermaphrodite duct that at first has a very narrow lumen, but its greater part is distended as a seminal vesicle. Hermaphrodite duct with a short, tapered distal section that enters the carrefour embedded at the base of the globular albumen gland (1.2 mm long), and gives rise to a talon comprising a spherical seminal receptacle on a elongated, narrow shaft. Spermooviduct with wide proximal section dominated by prostatic alveoli abutting the albumen gland, but greater part of its length dominated by oviductal glands, over which traverses a narrow band of prostatic alveoli to terminate in the vas deferens. Total length of spermooviduct

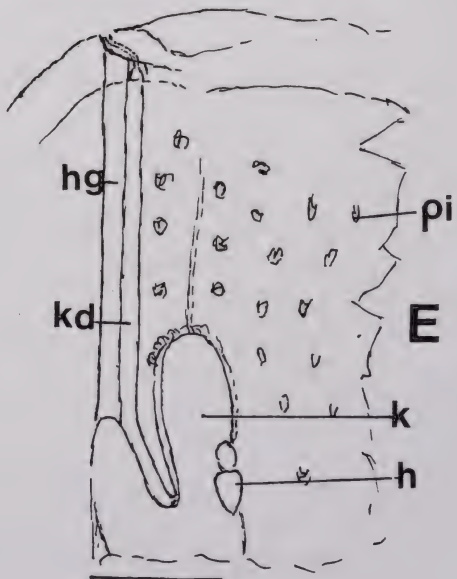
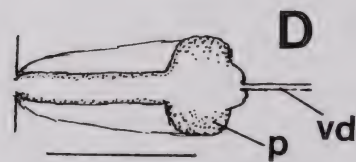
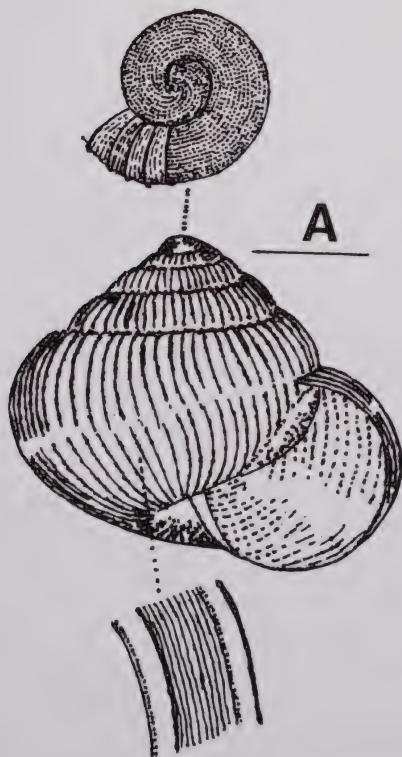
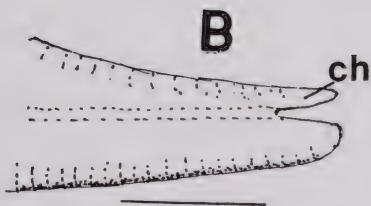
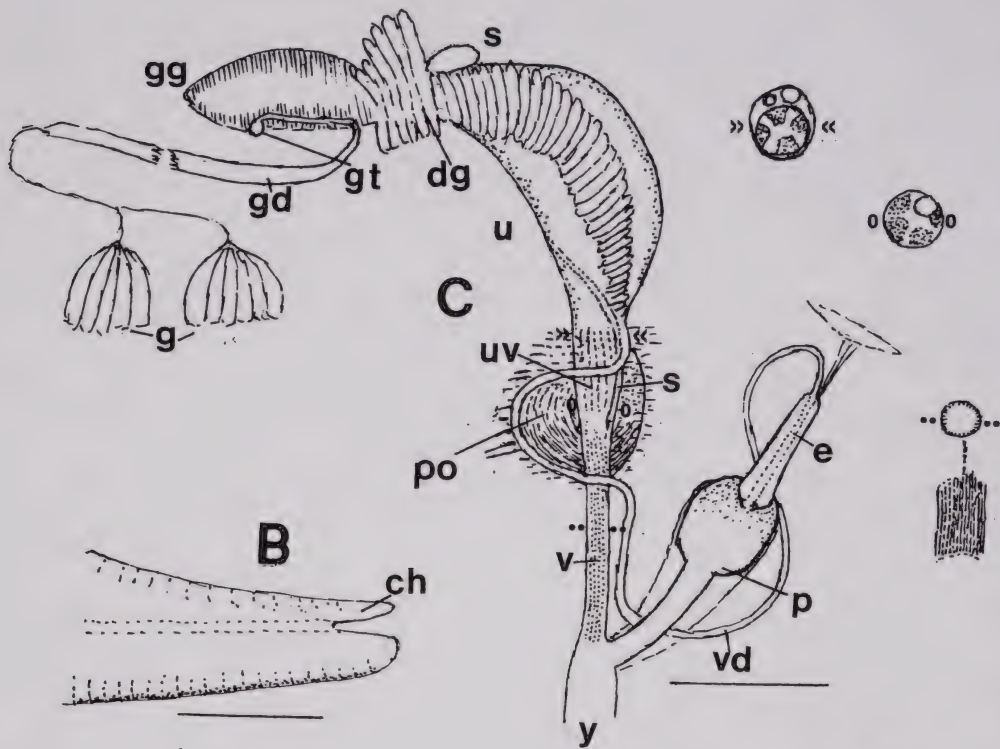


Table 1. Structural features of the shell of *Phenacohelix aurea* n. sp. based on measurements of representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	South Kaipara Head	2.8	2.5	4.8	0.2	0.2	0	32	50
2	South Kaipara Head	2.9	2.7	4.9	0.2	0.2	0	33	52
3	South Kaipara Head	3.2	2.8	5.2	0.6	0.5	0.2	40	68
4	Marakana	2.9	2.7	4.8	0.2				
5	Titirangi	2.6	2.4	4.5	0.2				
6	Parakao	3.0	2.8						
7	Parakao	3.0	2.8						
8	Lion Rock, Piha	3.0	2.4	4.8	0.5	0.5	0.2	39	72

1,2,3. AK154652, G.M. Barker; 4. AK151635, B.F. Hazelwood; 5. AK150874, J.F. Goulstone; 6,7. AK81264, A.W.B. Powell; 8. AK155642, B.F. Hazelwood.

1.6 mm. Free oviduct short (0.8 mm long), comprising a slightly bulbous, thick-walled tube (0.3 mm at widest) whose lumen comprises closely-packed longitudinal folds. Vagina long (up to 1.6 mm), rather slender, with fine, longitudinal, closely-spaced, raised ridges running internally. Free oviduct and proximal section of vagina in a pocket surrounded by a layer of connective, muscular tissue that is thickest and fleshy where it attaches to the proximal vagina. Pocket sometimes contains finger-like projections but no discernible opening could be found into the vagina. Vas deferens initially scribing a loop, ear-like in profile, usually fastened to the outside of pocket but sometimes partially embedded within the connective tissue. Remainder of vas deferens only weakly connected to terminal genitalia by connective tissue, terminating at apex of epiphallus. Spermathecal duct a fine tube, embedded in the surface of the free oviduct and spermooviduct for much of its length, before terminating in an oval sac (0.4 mm long) buried amongst the prostatic alveoli near the albumen gland. Epiphallus a thick, straight tube (0.8 mm long), with the short penial retractor muscle arising from its apex, adjacent to the entry of the vas deferens, to attach to the diaphragm near the kidney apex. Penis (1.1 mm long) comprises two sections, a proximal, bulbous chamber (0.5 mm long) into which protrudes the epiphallus apically (forming a vergic papilla), and a distal tubular section (0.6 mm long) with thick, muscular walls. The lumen of the penis is smooth but for some fine palisters and ridges around the vergic papilla. The condition in some specimens indicates that, during mating, the

Fig. 1 (opposite). Shell and anatomy of *Phenacohelix aurea* n. sp. Scale lines = 1 mm. A. Shell of holotype, AK73168. B-E. AK81264, Parakao. B. Posterior portion of foot. C. Reproductive organs. D. Everted penis. E. Pallial organs ventral view.

Abbreviations for Figs 1-11: b, buccal mass; be, oesophagus; br, buccal retractor muscle; ch, caudal horn; cr, columellar retractor muscle; dg, prostate gland; e, epiphallus; fs, foot grooves; g, ovotestis; gd, hermaphrodite duct; gg, albumen gland; gt, talon; h, heart; hg, hindgut; k, kidney; kd, ureter; mc, mantle collar; mg, mucous gland; mu, muscle; n, needle (dart); og, salivary glands; p, penis; pc, penial caecum; pg, pedal ganglia; pi, black or white pigment; po, pocket; pp penial pilaster; pr, penial retractor muscle; ps, penial sheath; rs, radula sac; s, spermathecal shaft and sac; ss, spermathecal duct and sac; u, spermooviduct; uv, free oviduct; v, vagina; vd, vas deferens; y, atrium.

penis contracts and the epiphallus protrudes into the penial lumen to present the vergic papilla at the distal extremity of the penis (Fig. 1D) before the penis is entirely everted.

Other Anatomy

Pallial cavity (3.1 mm long), with the mantle tissue possessing some black pigment that is easily visible through the shell of the live animal. Kidney bilobed, its pericardial lobe longer (1.5 mm long) than its rectal lobe. Ureter a closed tube for its entire length to terminate at excretory orifice near the pneumostome; primary and secondary sections forming V-shaped juncture between lobes of the kidney, with sections partially appressed in mature animals. Pericardium containing the heart (0.6 mm long) recessed into the lateral margin of the kidney.

REMARKS

The above description of the shell was based on the holotype. Eight specimens were dissected, some of which had been preserved in formalin and the shells partially dissolved. In the dissected snails there was considerable variation in the length of the epiphallus and the distal tubular section of the penis. Nonetheless, the solid, ovoid proximal section of the penis and the rigid, straight epiphallus were always present and therefore diagnostic. The pocket around the oviduct and proximal vagina, though varying in shape and size, was also a notable feature. The reproductive structures within the pocket were difficult to access during dissection due to the fibrous nature of the connective tissue. Solem (1982) described this as a 'vaginal pocket' but its exact function remains to be determined. One specimen dissected had the penis everted (Fig. 1D) with a section of slender vas deferens at its apex. Another had the narrow base of the spermathecal duct separate from the oviduct.

Solem (1978) published on the anatomy of *Phenacohelix* specimens obtained by Laurie Price from Kaitaia. This was not the species represented by the type specimen of *Phenacohelix pilula*. Instead it is *Phenacohelix aurea* n. sp. The anatomical findings of Solem (1978) and of the present study generally agree well.

TYPE LOCALITY

South Kaipara Head, Lake Ototoa Scenic Reserve, in fallen nikau fronds (*Rhopalostylis sapida*), 67 m, Q09 222215.

HOLOTYPE

AK73168, 3.3 mm x 2.9 mm, J.F. Goulstone 21/8/98.

PARATYPES

AK73169 (2), from type locality, J.F. Goulstone 21/8/98. MONZ 127803 (3), South Kaipara Head, G.M. Barker 21/10/78.

OTHER MATERIAL EXAMINED

Kaitaia O04 412814, L. Price 5/11/78, AK153503. **Maungataniwha** O04 589710 400 m, P.C. Mayhill 1/11/87, AK154662. **Mangatete Scenic Reserve** O04 446834 60 m, P.C. Mayhill 1/3/88, AK154690. **Paranui Scenic Reserve** O04 519811 110 m, P.C. Mayhill 1/9/87, AK154700. **Awanui** O04, AK64465. **Taipa** O04, A.W.B. Powell 1/1/50, AK82947. **Oruru Valley** O04 575824, J. Kenerdine, AK82970. **Mangamuka** O04 585703, J.F. Goulstone 1/1/69, AK82971. **Te Whau** P04 912721, N. Douglas 6/6/69, AK152145. **Waiare Rd.** P04 839748 70 m, P.C. Mayhill 1/11/87, AK154677. **Waiare Rd.** P04 841748 40 m, P.C. Mayhill 1/10/78, AK156012. **Herekino Gorge** N05, L. Fitzgerald 1/1/69, AK82972. **Mangamuka** O05 546674, D. Hole 17/3/72, AK154120. **Mangamuka** O05, A.W.B. Powell

1/1/38, AK829602. **Mangamuka** AK89026; O05 591614, N. Douglas 3/1/70, AK-L21050. **Mangataipa Scenic Reserve** O05 594615 20 m, P.C. Mayhill 1/1/91, AK154879. **Paihia** P05 972579, A.W.B. Powell 1/8/47, AK153694. **Puketū** P05 785603 220 m, P.C. Mayhill 1/10/86, AK154686. **Waipoua Forest** O06 623165, J.F. Goulstone 1/4/89, AK82964; AK82965; O06 2/5/68, AK82973; O06 623165, N. Douglas 29/12/68, AK-L21032; O06 623165, D. Hole 24/4/77, AK154311; O06, D.H. Graham 11/12/28, AK82948; O06 588213 365 m, N. Douglas 29/5/71, AK-L21152. **Yakas Track** O06 602181 240 m, P.C. Mayhill 1/1/90, AK156049. **Waiotemarama** O06 505298, J.F. Goulstone 1/4/89, AK-L3367; O06 505290, J.F. Goulstone 1/5/90, AK-L20900. **Opononi** O06, W. La Roche 1928, AK82951; O06, A.W.B. Powell 2/5/68, AK82955. **Waima Forest** O06 515345, J.F. Goulstone 1/5/90, AK-L10941. **Waimamakau R.** O06 486240, J.F. Goulstone 1/5/90, AK152559. **Mt Hikurangi** P06 934272 380 m, P.C. Mayhill 1/9/88, AK154877; P06 934269, P.C. Mayhill 1/10/86, AK156029. **Matapouri Bay** Q06 472258 N. Douglas 17/5/72, AK152121. **Whangarei** Q06 316121, J.F. Goulstone 17/1/95, AK96567. **Whangarei A.H. Reed Reserve** Q06 319108, J.J.F. Goulstone 17/1/95, AK-L20262. **Whangarei Falls** Q06 316121, J.F. Goulstone 17/1/95, AK-L20266. **Maunganui Bluff** O07 625035, J.F. Goulstone 1/4/89, AK96200. **Tangowahine** P07 928028, J.F. Goulstone 18/1/95, AK96524; P07 926922 A.W.B. Powell 28/10/47, AK82954 AK82978. **Parakao** P07, A.W.B. Powell, AK81264. **Tangiteroria School** P07 056973, J.F. Goulstone 18/1/95, AK96491. **Kirikopuni** P07 973046, J.F. Goulstone 18/1/95, AK96535. **Titoki** P07 087055, J.F. Goulstone 18/1/95, AK-L20267. **Dargaville** P07 814914, N. Douglas 3/1/70, AK-L21150. **Pakotai Scenic Reserve** P07 884092 80 m, P.C. Mayhill 1/9/87, AK154684. **Houto State Forest** P07 929028 60 m, P.C. Mayhill 1/2/80, AK156014; P07 944053 100 m, P.C. Mayhill 1/8/87, AK155971; P07 936028 300 m, P.C. Mayhill 1/9/84, AK156056. **Maropiu Forest** P07 819025 240 m, P.C. Mayhill 1/10/94, AK156065. **Parau Bay** Q07 426024, J.F. Goulstone 20/1/95, AK-L20260. **Coronation Reserve** Q07 296087, J.F. Goulstone 17/1/95, AK-L20261; A.W.B. Powell 16/12/68, AK-L2241. **Whangarei Heads** Q07, AK-L2245. **Mt Manaia** Q07 474967, B.F. Hazelwood 26/10/91, AK-L7842. **Waipu Caves** Q07 333840, B.F. Hazelwood & D. Watson 9/9/84, AK-L3393. **Whatiririri Scenic Reserve** Q07 154011 160 m P.C. Mayhill 1/7/96, AK154875. **Horokaka** Q07 133917 500 m, P.C. Mayhill 1/11/86, AK156020. **Maungatapere** Q07 185018 340 m, P.C. Mayhill 1/12/81, AK155978. **Waipu Gorge** Q07 332838 100 m, P.C. Mayhill 1/11/86, AK156052; Q08 356700, B.F. Hazelwood 1/4/91, AK(L)10220. **Tokatoka** P08 984712 160 m, P.C. Mayhill 1/10/87, AK155980. **Brynderwyn** Q08 393680, D. Hole 16/7/74, AK154474. **Arcadia Rd.** Q08 223704 120 m, P.C. Mayhill 1/7/87, AK155985. **Tinopai** Q09 237499, J.F. Goulstone 24/2/91, AK-L10078. **South Kaipara Head** Q09 223262 100 m, G.M. Barker 21/10/78, AK154652, AK154588. **Lake Ototoa Scenic Reserve** Q09 222215 67 m, J.F. Goulstone 21/8/98, AK155357. **Warkworth** R09 592328, B.F. Hazelwood 8/4/96, AK151647. **Dome Valley** R09 552363, B.F. Hazelwood 11/1/91, AK-L9401. **Moirs Hill** R09 583261, D. Hole 17/5/74, AK154097. **Omaha Valley Rd.** R09 654435, B.F. Hazelwood 4/6/90, AK150496. **Omaha Valley** R09 657420, B.F. Hazelwood 1/9/89, AK-L3396. **Matakana** R09 651376, B.F. Hazelwood 8/4/96, AK151635. **Omaha State Forest** R09 628415 180 m, P.C. Mayhill 1/8/87, AK156025. **Waitakere Ranges** Q11 & R11 many sites, AK64464, AK64466, AK82950, AK82952, AK82953, AK82956, AK82958, AK82960, AK82963, AK82967, AK82968, AK82969, AK82974, AK82975, AK82976, AK82977, AK150874, AK154257, AK154459, AK155641, AK155642, AK-L20494, AK-L21471, AK-L21613, AK-L3283, AK-L3287, AK-L4340. **Waiuku** R12, Rev. W.H. Webster, AK42827, AK25706, AK82966. **Waiuku** A.W.B. Powell 24/7/27, AK82961. **Waipipi Scenic Reserve** R12 580412 50 m, J.F. Goulstone 1/12/76, AK82959, 31/10/97, AK154268. **Paerata Scenic Reserve** R12 788462, J.F. Goulstone 1/10/85, AK-L2308. **Colebaker Ridge** R13 670235 200 m, P.C. Mayhill 1/6/83, AK155548.

DISTRIBUTION AND HABITAT

Phenacohelix aurea n. sp. is distributed from Kaitia to West Auckland, and down the west coast to just south of Waikato Heads. The species does not appear to be present in eastern districts of Auckland or in the Hunua Ranges. It is essentially a litter-dweller, achieving high abundance in certain habitats, such as among the basalt boulders at Maunganui Bluff. *P. aurea* is often readily found in litter under kawakawa (*Macropiper excelsum*), karaka (*Corynocarpus laevigatus*), puriri (*Vitex lucens*) and other broadleaf trees and shrubs, and in the fallen fronds of

nikau. The apparent abundance in the Waitakere Range suggested by the amount of material in the Auckland Museum reflects the extent of collecting there over many years, rather than true relative abundance.

Phenacohelix brooki n. sp.

Figs 2, 12

ETYMOLOGY

Named for Fred J. Brook of Whangarei.

DESCRIPTION

Shell

Small, depressed globose, moderately perforate, columella not reflected over umbilicus. Holotype shell 4.6 mm x 2.9 mm, with four and three-quarters, tight whorls. Protoconch smooth, 1.5 whorls, 0.2 of total shell width. Umbilicus 0.2 of total shell width. Teleoconch whorls with close-spaced primary axials, 50 on the first teleoconch whorl, 100 on the final whorl, each broader and strongly constructed at the base, sharp at apex. Interstices with indistinct crowded axial ridges, with occasional tall and very weak spiral lirae that do not impinge greatly on the primary axials. Axials arising at right angles from moderately deep sutures and running very straight on dorsal aspect of the whorl, but becoming sinuous underneath. Background colour very pale brown 10/YR/8/3. Dorsal surface has broad bands, with some finer zigzags and spots between, of reddish brown 5YR/4/3. Ventral surface has fine reddish brown zigzags terminating in the umbilicus.

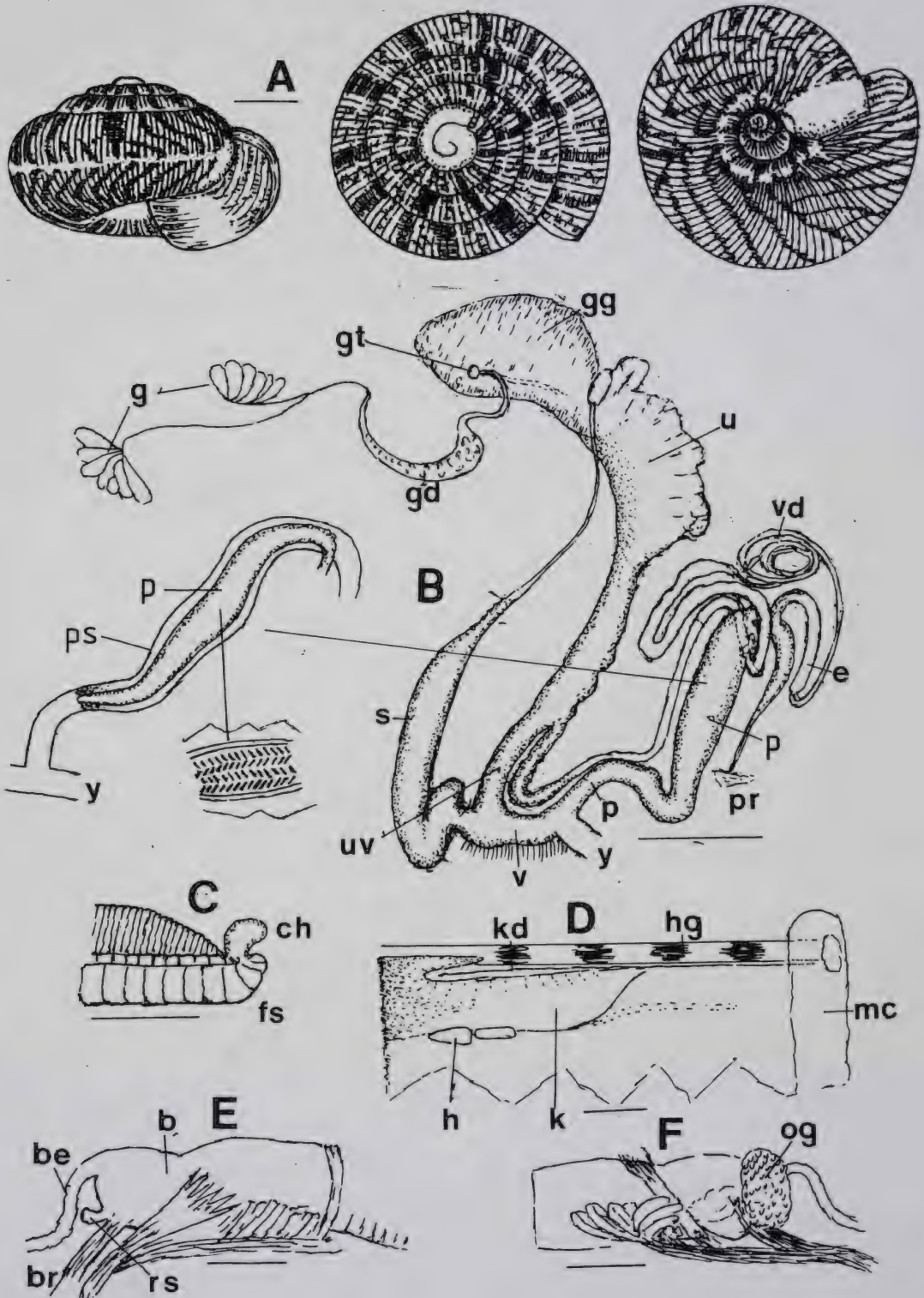
External Morphology

Foot posterior produced to a pronounced caudal horn, but caudal foss only shallow. Foot margin strongly crenellated, surmounted by two pedal grooves.

Reproductive Anatomy

Ovotestis comprising two, discrete clumps of alveoli. Hermaphrodite duct initially very slender; then expands rapidly for 1.1 mm to form a distended, sickle-shaped seminal vesicle; finally narrows to a short section that turns posteriorly to terminate in the carrefour embedded in the ventral surface of the albumen gland. Carrefour yielding a spherical talon, 0.14 mm in diameter. Spermooviduct 2.6 mm long, its proximal half distended, with thick prostatic alveoli and oviductal glands, distal half narrowed to a thick-walled tube. Free oviduct (1 mm long) slightly narrower than distal spermooviduct. Vagina short (0.8 mm). Spermathecal duct long (2.6 mm), distended for approximately half its length, then abruptly narrowing to a fine tube, attached to proximal spermooviduct by connective tissue, and terminating in a small, oblong sac (0.7 mm long) resting against the albumen gland. Vas deferens a very long tube, with a short, thick-walled section where it exits spermooviduct; otherwise thin-walled, most of its length extensively convoluted and coiled, and fastened firmly to the spermooviduct with many layers of fibrous

Fig. 2 (opposite). Shell and anatomy of *Phenacohelix brooki* n. sp. Scale lines = 1 mm (A, B, D) or 0.5 mm (C, E, F). A. Shell of holotype, AK73170. B. Reproductive organs, AK81264. C. Posterior part of foot. D. Pallial organs, ventral view. E. Right-hand side of buccal mass showing retractor muscle attachment. F. Left-hand side of buccal mass showing salivary gland. For key to abbreviations, see Fig. 1.



tissue. Vas deferens terminating at apex of a short, thicker-walled epiphallus. Penis long (1.3 mm), narrow at its proximal apex but broad (0.3 mm at widest) in its middle section below entry of epiphallus, before narrowing slightly to the uniformly tubular distal section. Penis enclosed in a thin sheath. Lumen of penis with multiple rows of short, low, herring-bone ridges over its entire length. Penial retractor muscle fastened to diaphragm near mantle collar.

Other Anatomy

Pallial cavity (7.4 mm long) with considerable black pigment. Kidney with strong pericardial lobe (4.3 mm long) and weak rectal lobe, with no space between kidney and hindgut; ureter running along anterior face of kidney and then along hindgut to excretory orifice at mantle collar. Heart, 0.7 mm long, orientated parallel to long axis of mantle cavity. Buccal mass with very strong retractor muscle fastened prominently along its whole length. Oesophagus entering buccal mass apically, with salivary glands clustered around.

REMARKS

The shell description presented above is based on the holotype. The only animal dissected, a paratype from the type locality, had a shell of 5.2 mm x 3.0 mm, four and a half whorls, with the protoconch 1.1 mm in diameter, last whorl at aperture 1.1 mm in width, first teleoconch whorl with 48 primary axials, the last teleoconch whorl with 106 axials, and with the umbilicus 0.6 mm in diameter.

The shell of *Phenacohelix brooki* n. sp. is remarkably like that of *P. giveni* in size, shape and colour pattern. However, when shells of these two species are viewed side by side the shell of *P. brooki* is consistently smaller, with tighter whorls, and the axials, viewed from the top of the shell, arise at right angles from the suture and maintain that direction with only slight sinuousness to the perimeter. The axial ribs of *P. giveni*, by contrast, slope steadily away from the direction of shell growth. The reproductive anatomy of the two species exhibit numerous differences.

TYPE LOCALITY

Northland, Whangamumu, Karaka Point. Q05 288593–287595.

HOLOTYPE

AK73170, 4.6 mm x 2.9 mm, F.J. Brook 5/11/94.

PARATYPES

AK73171 (4) from type locality, F.J. Brook 5/11/94. MONZ 127801 (2) Whangamumu, Karaka Point Q05 288593, F. Brook 19/9/94.

OTHER MATERIAL EXAMINED

Whakaangi O04 621949 320 m, P.C. Mayhill 1/2/91, AK154663. **Cape Brett** Q05 321685 100 m, F.J. Brook 30/8/93, AK82775; Q05 265620 160 m, P.C. Mayhill 1/11/88, AK154890; Q05 265622 160 m, P.C. Mayhill 1/11/88, AK156015. **Deep Water Cove** Q05 299664, F.J. Brook & J.F. Goulstone 8/12/93, AK154061. **Whangamumu** Q05 281597, A.W.B. Powell 27/9/66, AK154062; Q05 277601 140 m, P.C. Mayhill 1/8/87, AK154860; Q05 280600 80 m, P.C. Mayhill 1/4/81, AK154864. **Ngaioitonga** Q05 237545 140 m, P.C. Mayhill 1/3/96, AK156036; Q05 198488 150 m, P.C. Mayhill 1/10/78, AK156009. **Moturua I.** Q05 188638 70 m, P.C. Mayhill 1/5/81, AK155992.

DISTRIBUTION AND HABITAT

Found with *P. giveni* in litter on the ground, particularly in fallen nikau fronds. The present

known distribution of this snail is very small, all sites near the Bay of Islands except one at Whakaangi in Doubtless Bay.

Phenacohelix giveni (Cumber, 1961)

Figs 3, 12

DESCRIPTION

External Morphology

Margin of foot crenellated, thin, white. Only one pedal groove evident, terminating posteriorly in a caudal foss above which is a pronounced caudal horn. Posterior of foot dark grey to black in dorsal aspect. Head region around and behind ommatophores black.

Reproductive Anatomy

Ovotestis comprising two clumps of finger-like alveoli. Hermaphrodite duct initially slender, then produced to a short, distended section (1 mm long) functioning as a seminal vesicle, then reducing to very short thin tube terminating in the carrefour, and a ovoid talon (0.3 mm long) embedded in the albumen gland. Albumen gland large (2.1 mm long), globular, comprising coarse, crowded alveoli. Spermooviduct ovoid (3.5 mm), with thin band of prostatic alveoli along its entire length, though sometimes wider proximally. Free oviduct a thick tube (1.7 mm long). Vagina absent as both the spermatheca and free oviduct arise from the atrium. Spermathecal duct rather broad proximally, but rapidly narrowing to a very slender duct that terminates in a small, oval sac lying against the base of the albumen gland. Vas deferens emerging from distal extremity of the spermooviduct as fine tube, passing close to atrium through angle of oviduct and penis, to abruptly terminate at the apex of the epiphallus. Epiphallus tubular, comprising two sections of approximately equal length: a thick-walled, proximal section, and a narrower, thin-walled distal section, the latter entering the apex of the penis adjacent to the insertion of the penial retractor muscle. Main body of penis comprising a tubular, somewhat irregularly-shaped proximal section, bearing internally small papilla of which many are armed with crystalline spines orientated towards the atrium, and a slightly narrower, uniformly tubular distal section that evidently has a smooth internal surface. The proximal penis bears a prominent lateral caecum that is initially tubular but terminates in a somewhat bulbous, solid apex. The tubular section of the penial caecum is internally lined mostly with a thick folded epithelium, but for a broad channel running to the penis proper and whose epithelium is produced into small, rounded papillae that carry spines orientated toward the caecal apex. The bulbous apex comprises a chamber packed with fibrous, muscular material, in which is embedded the bulbous base of a hollow dart and associated keyhole-shaped structure. The shaft of the dart produces into the lumen of the penial caecum. Opening into the caecal apex, opposite the keyhole-shaped structure, is a singular, elongate gland, the apex of which is firmly attached to the outer wall of the penial caecum by a short tuft of muscle fibres. The penial caecal complex is of variable length, sometimes barely extending beyond the apex of the penis proper, sometimes stretching far beyond and dwarfing the penis. Penis, and base of the penial caecum, enclosed in a well-developed sheath. The penis retractor muscle arises from the diaphragm in the mid section of the pallial cavity.

Other Anatomy

Pallial cavity 8.5 mm long, kidney 3.5 mm long, heart 1.2 mm long, mantle collar 0.9 mm wide. Pericardial lobe of kidney large, rectal lobe very small. Ureter V-shaped, firstly running

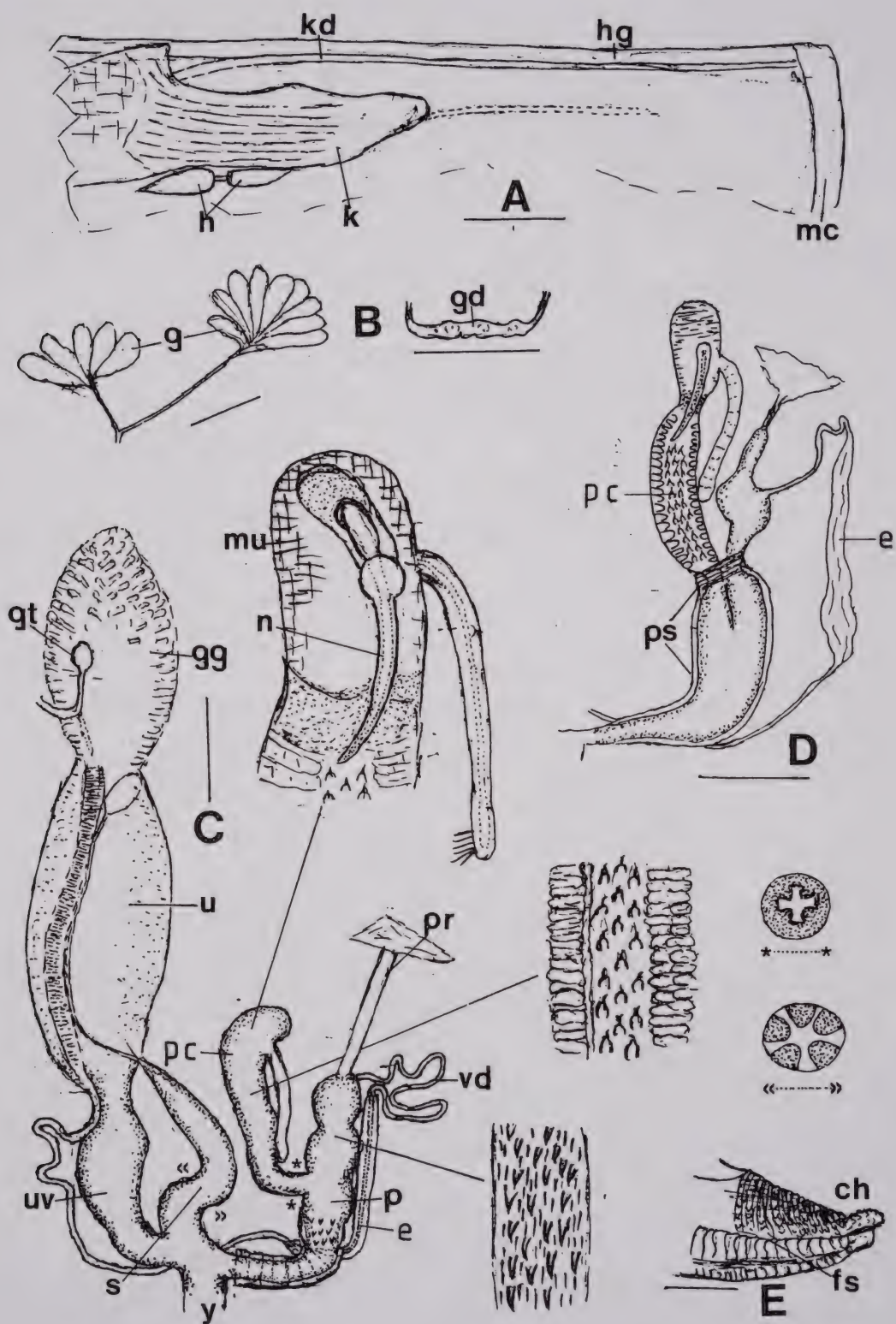


Table 2. Structural features of the shell of *Phenacohelix giveni* (Cumber, 1961) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	Mimiwhangata	5.4	3.5						
2	Wiri	4.8	3.1	4.5	1.1	1.1	0.7	31	75
3	Awakino	4.9	2.8	4.3	1.1	1.1	0.7	37	72
4	Tongaporutu R.	5.3	3.4	4.8	1.1	1.1	0.7	35	70
5	Tongaporutu R.	5.6	3.9	4.8	1.1	1.5	0.6	45	86
6	Pukerimu	6.2	3.4	4.8	1.1	1.3	0.8	41	83
7	Kawau Pa	4.7	3.1	4.3	1.1	1.3	0.6	44	76
8	Lake Tarawera	5.0	2.7	4.8	1.0	1.1	0.6	41	82
9	Lake Tarawera	6.3	4.0	4.8	1.1	1.9	0.6	45	103
10	Waitomo	6.3	3.9	5.0	1.0	1.6	0.8	39	92
11	Lake Rotoiti	5.0	3.2	4.8	1.1	1.3	0.6	46	84

1. AK15215, Q06 369379, F.J. Brook & J.F. Goulstone 20/4/94. 2. AK154039, R11 735633 J.F. Goulstone 7/7/87. 3. AK154569, R17 509807, J.F. Goulstone 7/3/97. 4. AK153580, Q18 485644, J.F. Goulstone & R. Prasad 9/3/97. 5. AK154043, Q18476641, J.F. Goulstone 7/3/97. 6. AK154562, U16 747288 500 m, P.C. Mayhill 1/5/97. 7. AK154569, Q18 490690, J.F. Goulstone 10/3/97. 8, 9. AK154590, 38°11'S 176°26'E, G.M. Barker 1/1/80. 10. AK154821, 37°16'S 175°01'E, G.M. Barker 19/9/78. 11. AK154054, V15 137478 380 m, P.C. Mayhill 1/8/97.

along anterior face of the kidney, emerging from kidney tissues before rectal lobe to run adjacent to rectum and open to exterior just behind anus at respiratory pore. Wall of pallial cavity clearly visible between two arms of ureter. Oesophagus exits from the roof of the buccal mass forward of median, dorsal position.

REMARKS

I dissected eleven specimens, whose shell dimensions are given in Table 2. The dart at the apex of the penial caecum was fully preserved in every animal dissected and thus is probably not expendable. The whole penial caecum apparatus looks as if it may function as a syringe. Although the shells of the eleven dissected specimens varied, particularly in the number of ribs, the animals showed only penial variations that were caused by deformities in the penial sheath.

DISTRIBUTION AND HABITAT

Phenacohelix giveni is found throughout much of the North Island, but is absent at Te Pahi in the Far North. It is generally an abundant snail in the northern half of the North Island. It can be found easily in fallen nikau fronds, but also in a wide range of litter types, and among rocks.

Fig. 3 (opposite). Anatomy of *Phenacohelix giveni* (Cumber). Scale lines = 1 mm (A, C) or 0.5 mm (B, D, E). A, B, C, E. AK154039, Wiri. D. AK154562, Pukerimu. A. Pallial organs, ventral view. B. Ovotestis and enlarged portion of hermaphrodite duct. C. Reproductive organs. D. Penis and penial epiphallus showing the effect of a deformed penial sheath. E. Posterior portion of foot. For key to abbreviations, see Fig. 1.

It also lives arboreally in nikau trees. Where bush has been trampled by stock in farm lots, and subsequently fenced, it is one of the first species to reappear on the ground. In the southern half of the North Island it is not so abundant, and in some local areas, for example in the Wairarapa, appears to be absent.

Phenacohelix hakarimata n. sp.

Figs 4, 12

Phenacohelix ponsonbyi of authors, not of Suter, 1897.

ETYMOLOGY

Named for the range of hills that contains the type locality.

DESCRIPTION

Shell

Small (6.4 mm x 3.9 mm), depressed globose, four and a quarter whorls, final whorl 0.2 of total shell diameter, height of spire half height of aperture. Protoconch 0.9 mm wide, 1.1 whorls, 0.15 of total shell diameter, with faint, spiral lines. Umbilicus 0.7 mm wide, 0.12 of total shell diameter. Teleoconch with closely spaced axial ribs emerging at right angles from suture, then, on dorsal surface, arcing gently away from direction of shell growth, becoming slightly sinuous on ventral surface. First teleoconch whorl has 37 axials, the last whorl 77 axials. Interstices with fine, closely-spaced secondary axials, crossed by spiral striae of about equal strength. Base colour very pale brown 10YR/8/3 superimposed with flashes and zigzags of reddish brown 5YR/4/3 all over.

External Morphology

Foot margin strongly crenellated, with two pedal grooves above. Posterior of foot without caudal horn, finely grooved on dorsal surface.

Reproductive Anatomy

Ovotestis has two clumps of finger-like alveoli. Hermaphrodite duct starts as very slender tube, but for most of its length (2.5 mm) is distended as a straight seminal vesicle, reducing briefly before entering albumen gland, terminating in carrefour and talon. Albumen gland (1.5 mm) small, evidently very depleted in the dissected specimens. Spermooviduct (2.3 mm long x 1.2 mm wide) sickle-shaped, prostatic alveoli confined to proximal quarter. Free oviduct (2.5 mm x 0.5 mm) thick, folded. Spermathecal duct (1.3 mm long) broad at base, with same diameter as free oviduct, but tapering to a slender tube which terminates in an oblong sac about 0.8 mm long resting against albumen gland. Vagina (1.8 mm long) proximally bulbous reducing to thick tube (0.4 mm wide) before entry to atrium. Vas deferens broad at its origin from distal spermooviduct but soon becomes slender to pass through angle of vagina and penis before entering penis just below apex. Vas deferens continues internally within the penis and open a third of the way down from apex. Penial retractor muscle arising from diaphragm about half way along

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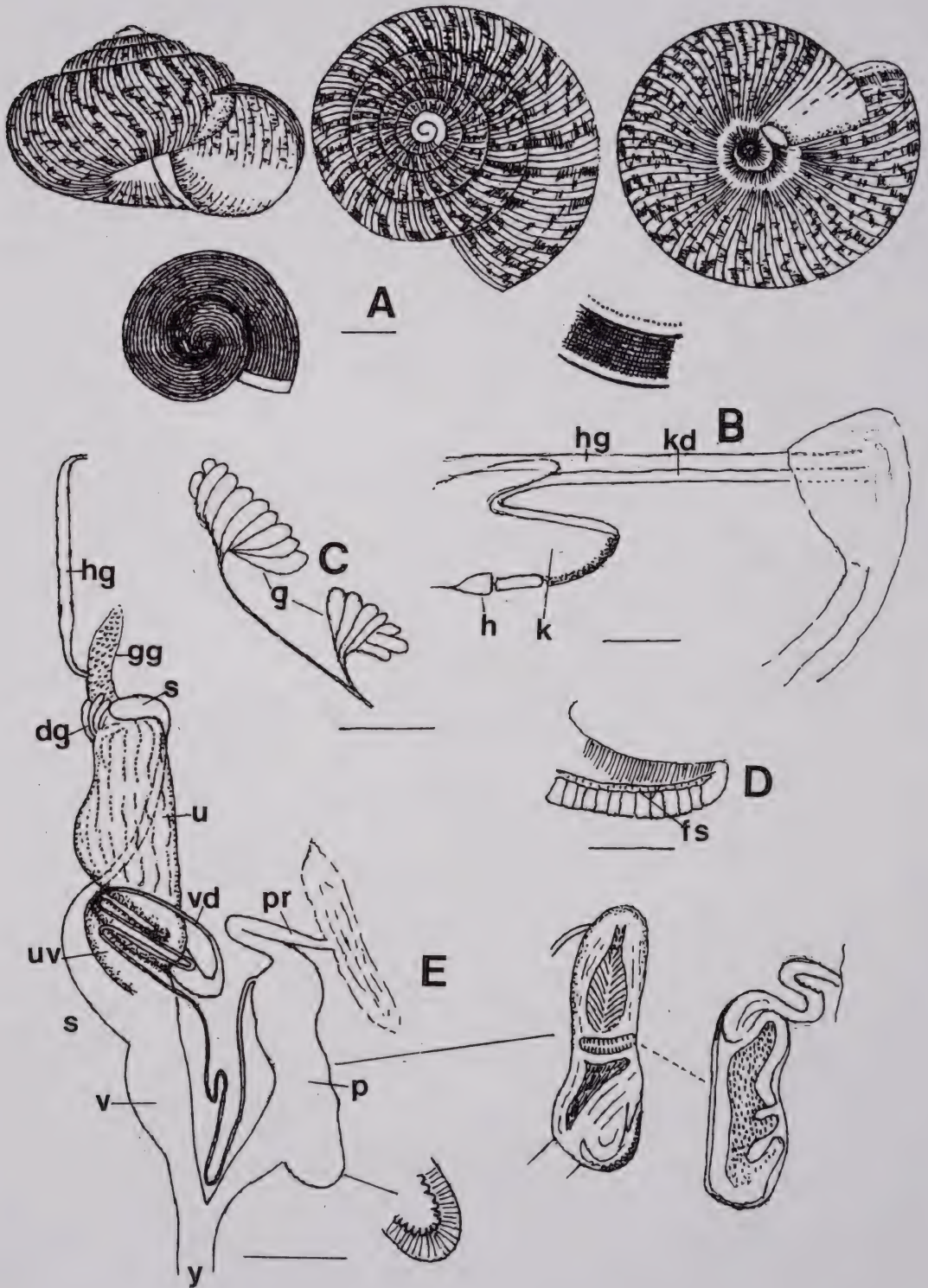


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Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	Hakarimata	5.9	3.1	4.3	0.9	1.2	0.7	37	77
2	Kaimai	5.5	3.0	4.5	0.9	1.2	0.9	40	106
3	Kaimai	4.3	2.9	4.0	0.7	1.2	0.6	38	84
4	Kaimai	5.2	3.4	4.3	0.8	1.3	0.7	35	83
5	Kaimai	4.3	2.7	4.0	0.9	1.0	0.6	36	76
6	Pirongia	6.4	3.9	4.8	0.9	1.7	1.0	43	117

1. AK154591. 2. AK154579. 3. AK154578. 4. AK154646. 5. AK154592. 6. AK154599. All collected by G.M. Barker.

pallial cavity, to attach at the apex of penis. Penis has elongate, globular proximal section (2.5 mm long x c. 1 mm wide) and distal reducing tubular section, half width of vagina at entry to the atrium. Proximal section of penis has internal irregular protuberances and mixture of low herringbone ridges and short crowded pilasters covering the thick walls. Before entry to the distal penis, this section bulbous, containing fleshy portion with short papillate pad enclosing small semi-circular space with low ridges.

Other Anatomy

Pallial cavity 9.3 mm long, kidney 2.7 mm long, heart 1.6 mm long, mantle collar 1.4 mm wide. Pericardial lobe of kidney large, triangular. Rectal lobe of kidney substantial, narrowly triangular. Ureter starts from apex of pericardial lobe of kidney, follows anterior face of both pericardial and rectal lobes, then follows hindgut to orifice just behind it at the respiratory pore. There is wide space between the reflexed arms of the ureter. There are spots of black pigment over pallial cavity membrane and tip of digestive gland. Oesophagus and saliva ducts enter posterior extremity of the buccal mass, just above the radula sac.

REMARKS

The shell description is of the holotype. The anatomy is based on a composite of the six dissected animals, but substantially on the dissected animal from the type locality. One of the dissected animals (3 Kaimai; Table 3) was sexually immature, without developed genitalia. Another (5 Kaimai) had the reproductive organs formed, albeit small, and only the proximal third of the penis lumen had pilasters. In this young specimen it was easier to see that the vas deferens, though entering near the penial apex, in fact emptied into the penis one third of the way down. All mature specimens dissected had the bulge just before the narrower distal section of the penis, but the function of the partly enclosed space could not be determined.

Phenacohelix hakarimata resembles *P. ponsonbyi* in shell morphology. Whereas *P. ponsonbyi* shells have clearly defined, sharp lirae on the protoconch, those of *P. hakarimata* possessed lirae on the protoconch that were often hard to discern. The lirae were particularly difficult to see in specimens of *P. hakarimata* from the eastern parts of its range. Identification often relies on the recognition of the single-whorled, pointed protoconch in *P. hakarimata*, as opposed to the 1.5

flat whorls in the protoconch of *P. giveni*. The penial complex, however, is clearly different in these two species.

TYPE LOCALITY

Hakarimata Range, S14 973896, 158 m.

HOLOTYPE

AK73172 5.4 mm x 3.8 mm, P.C. Mayhill 1/1/84.

PARATYPES

AK 73173 (14) from type locality, P.C. Mayhill 1/1/84. MONZ 127802 (10) from type locality, P.C. Mayhill 1/1/84.

OTHER MATERIAL EXAMINED

Korapuki Is. T10 648005 40 m P.C. Mayhill 1/3/94, AK156158. Hot Water Beach T11 618754 10 m, P.C. Mayhill 1/9/77, AK156043. Waiomu T11 362608 180 m, P.C. Mayhill 1/3/81, AK156186. Kauaeranga Valley T12 556455, J.F. Goulstone 1/1/79, AK152292; T12 481570, J.F. Goulstone 1/1/79, AK152317. Kopu-Hikuai Rd. Summit T12 478468, J.F. Goulstone 5/1/79, AK152347. Waikawau Cave Reserve R13 689097 60 m, P.C. Mayhill 1/12/78, AK155555. Parakiwai T12 619317 100 m, P.C. Mayhill 1/11/80, AK156022. Te Aroha T13 506028, J.F. Goulstone 5/1/97, AK-L21258. Waitengaue Stream T13 633069 100 m, P.C. Mayhill 1/11/96, AK155402. Waitengaue Track T13 623067 120 m, P.C. Mayhill 1/3/97, AK155545. Maratoto Valley T13 559279 200 m, P.C. Mayhill 1/11/78, AK156077. Komata Reef T13 538226 240 m, P.C. Mayhill 1/1/79, AK156087. Waitawheta T13 561100 200 m, P.C. Mayhill 1/9/82, AK156113; T13 559083, P.C. Mayhill 1/11/96, AK156116. Wairongomai T13 545027 320 m, P.C. Mayhill 1/9/79, AK156133. Waihi Beach N. end U13 703188, N. Douglas 20/6/71, AK152986. Cogswell Rd. R14 893773 100 m, P.C. Mayhill 1/7/78, AK155425. Hamilton S14 126784, G.M. Barker 2/8/78, AK154634. Hakarimata, Waingaro S14 973896 158 m: P.C. Mayhill 1/1/84, AK155269; P.C. Mayhill 1/9/83, AK155289. Hakarimata S14 006967 200 m, P.C. Mayhill 1/8/83, AK155273, 1/12/82, AK155315, 1/9/83, AK155322; S14 973892 60 m, P.C. Mayhill 1/4/79, AK155530. Whewells Bush S14 200728 52 m, P.C. Mayhill 1/1/84, AK155272, 1/10/84, AK155281, 1/11/84, AK155306. Pukemokemoke S14 198988 102 m, P.C. Mayhill 1/3/83, AK155294, 1/1/84, AK155293. Taupiri S14 034974 160 m, P.C. Mayhill 1/1/78, AK155467; H. Suter AK83082. West of Taupiri S14, L. Fitzgerald 1961, AK83079. Four Brothers Scenic Reserve S14 927728 180 m, P.C. Mayhill 1/7/83, AK155538. Upper Kaimai, Aongatete T14 681881 180 m, P.C. Mayhill 1/11/87, AK155824; T14 671879 180 m, P.C. Mayhill 1/12/88, AK155885. Abseil Rock T14 614951 500 m, P.C. Mayhill 1/12/86, AK156189. Wairere Falls T14 655814 420 m, P.C. Mayhill 1/1/81, AK155836. Tuahu Track T14 624961 400 m, P.C. Mayhill 1/4/97, AK155831. Te Tapui T14 412733 260 m, P.C. Mayhill 1/8/81, AK155810; T14 452707 340 m, P.C. Mayhill 1/12/84, AK155831. Mt Eliza T14 623922 280 m, P.C. Mayhill 1/3/88, AK156145. Te Tuhi Track T14 677787 520 m, P.C. Mayhill 1/3/86, AK156171. Lower Kaimai U14 795746, G.M. Barker 9/9/78, AK154641. Kirikiri Dam U14 982734 200 m, P.C. Mayhill 1/2/95, AK155854. Puketoki Scenic Reserve U14 734808 260 m, P.C. Mayhill 1/4/90, AK155875; U14 736810 260 m, P.C. Mayhill 1/12/88, AK155916. Kawhia-Raglan R15 737508 60 m, P.C. Mayhill 1/11/79, AK155411. Andersons Bluff R15 814451 110 m, P.C. Mayhill 1/8/77, AK155413. Bridal Veil Falls R15 774645 200 m, P.C. Mayhill 1/4/78, AK155419. Pirongia State Forest Park R15 875408 300 m, P.C. Mayhill 1/10/83, AK155572. Hauturu Rd. R15 878404 300 m, P.C. Mayhill 1/12/79, AK155397. Walter Scott Reserve S15 935454 260 m, P.C. Mayhill 1/7/78, AK155400; T15 326683 210 m, P.C. Mayhill 1/9/85, AK155275. Maungakawa No. 1 T15 325686 200 m P.C. Mayhill 1/9/85, AK155309, 1/3/85, AK155313, 1/4/85, AK155325. Maungakawa No. 2. T15 326683 210 m, P.C. Mayhill 1/2/82, AK156058. Maungatautari T15 365524 320 m, P.C. Mayhill 1/11/78, AK155462. Fitzgerald Glade T15 636577 280 m, P.C. Mayhill 1/7/81, AK156152. Selwyn Reserve T15 665513 280 m, P.C. Mayhill 1/7/81, AK156166. Hanga Rd. U15 717645 400 m, P.C.

Mayhill 1/8/87, AK155796. **Mangatoī Rd.** U15 966623 300 m, P.C. Mayhill 1/3/96, AK156054; U15 959628 300 m, P.C. Mayhill 1/3/96, AK156108. **Woods Mill** U15 711484 500 m, P.C. Mayhill 1/2/84, AK156163. **Mamaku, Galaxie Rd.** U15 777479 560 m, P.C. Mayhill 1/1/82, AK156177. **Rotoiti Scenic Reserve** V15 166486 300 m, P.C. Mayhill 1/11/86, AK156156. **Okataina** V15 116414 380 m, P.C. Mayhill 1/10/84, AK156169. **Ohope Scenic Reserve** W15 644578 40 m, P.C. Mayhill 1/8/79, AK155838. **Kotare Scenic Reserve** W15 714410 80 m, P.C. Mayhill 1/7/93, AK155857. **Motu River** X15, A.E. Brookes, AK155354, L4220. **Opotiki Waterworks** X15 925456 20 m, P.C. Mayhill 1/9/80, AK155816. **Waitomo, Stubbs Cave** R16 834246 340 m, P.C. Mayhill 1/7/78, AK155301. **Tawerau State Forest** R16 828197, P.C. Mayhill 1/8/81, AK155387. **Tawerau State Forest Ecological Reserve** R16 765203 240 m, P.C. Mayhill 1/1/84, AK155389. **Waitomo** S16 946250 G.M. & M.P. Barker, AK154825; S16 945250, G.M. Barker 1/9/89, AK154637; S16 945250 91 m, G.M. Barker 1/9/89, AK155505. **Hamilton Junior Naturalists' Club, Kawhia** 1/1/70, AK155253. **Waitomo, nr. Te Anga Rd.** S16 954198, G.M. & M.P. Barker 2/7/78, AK155374. **Ruakuri** S16 818249 260 m, P.C. Mayhill 1/5/84, AK155406. **Pukerimu Reserve** T16 698273 400 m, P.C. Mayhill 1/4/78, AK156181. **Hora Hora** U16 816288 600 m, P.C. Mayhill 1/11/81, AK156192. **Waimana** W16 694155, J.F. Goulstone 1/5/75, AK83083. **Marawaiwai** W16 883377 40 m, P.C. Mayhill 1/12/96, AK155785. **Hukutaia Domain** W16 844394 60 m, P.C. Mayhill 1/9/80, AK155812; W16 844394 60 m, P.C. Mayhill 1/8/79, AK155818. **Waimana, Wai-iti Track** W16 708133 410 m, P.C. Mayhill 1/4/79, AK155822. **Waioeka-Opotiki** W16 884377 60 m, P.C. Mayhill 1/7/86, AK155815; W16 882378 60 m, P.C. Mayhill 1/7/91, AK155829. **Te Pona a Pita Track** W16 707133 380 m, P.C. Mayhill 1/12/96, AK155863; W16 713133 380 m, P.C. Mayhill 1/12/96, AK155918. **Pakihi Track** X16 994309 120 m, P.C. Mayhill 1/12/94, AK155840. **Whareorino State Forest** R17 609078 340 m, P.C. Mayhill 1/3/83, AK155404; R17 593913 380 m, P.C. Mayhill 1/3/83, AK155409. **Pureora, Hurakia Block** T17 246840, J.F. Goulstone 1/4/82, AK150400, AK150485. **Pureora Information Centre** T17 331954, J.F. Goulstone 1/4/82, AK150351. **Whakatane River** W17 595927, J.F. Goulstone 1/5/77, AK-L20023. **Waikare River** W17 620973, J.F. Goulstone 1/5/79, AK-L20031. **Mangatawhero Stream** W17 580917, J.F. Goulstone 1/5/79, AK-L9096. **Ngatuoha** W17 721083 500 m, P.C. Mayhill 1/9/80, AK155879. **Mt Messenger** Q18 481546, J.F. Goulstone 8/3/97, AK-L21393; Q18 488553, J.F. Goulstone 8/3/97, AK-L21401. **Mokau Scenic Reserve** R18 553764, J.F. Goulstone 10/3/97, AK-L21414. **Waiau River, Parahaki Hut** V18 449660, J.F. Goulstone 1/5/81, AK150727. **Te Waiotekapiti Stream** V18 468610, J.F. Goulstone 1/5/81, AK151001. **Whirinaki** V18 275607, J.F. Goulstone 1/6/91, AK96195; V18 321725 400 m, P.C. Mayhill 1/4/84, AK155573. **Minginui** V18 355825 700 m, P.C. Mayhill 1/4/77, AK155801. **Waikaremoana** W18 570632, J.F. Goulstone 1/11/84, AK-L9400. **Between Te Puna & Marauiti Huts** W18 584636, J.F. Goulstone 1/5/81, AK151037. **Marauiti Hut** W18 570632; J.F. Goulstone 1/5/84, AK151057, J.F. Goulstone 1/5/80, AK151058. **Whanganui Hut** W18 613680, J.F. Goulstone 1/5/76, AK151207, AK83071. **Whanganui Track** W18 614683 700 m, P.C. Mayhill 1/2/82, AK155808. **Moerangi Track** Y18 324730 420 m, P.C. Mayhill 1/4/84, AK155785. **New Plymouth, Huatoki Domain** P19 036353, J.F. Goulstone 1/12/88, AK97943. **Tarata State Forest** Q19 268245 200 m, P.C. Mayhill 1/11/84, AK155493. **Pipiriki South** R21 864894 140 m, P.C. Mayhill 1/11/78, AK155573, AK155498. **Ihupiri Park** R22 897585 480 m, P.C. Mayhill, AK155557. **Aramaho** R22, W. La Roche 1928, AK95912.

DISTRIBUTION AND HABITAT

The preserved specimens dissected were all collected in *Freyinetia*. Others were found on the ground in litter, particularly fallen epiphytes and nikau fronds. *Phenacobelix hakarimata* has a wide range in the central North Island from south of Auckland, southern Coromandel Ranges to East Cape, northern Taranaki and Wanganui.

Phenacohelix lucetta (Hutton, 1884)

Figs 5, 12

DESCRIPTION

External Morphology

Animal mostly white. Foot moderately thick and margin crenellated, surmounted by two pedal grooves that terminate posteriorly in a shallow foss and attendant low caudal horn. Dorsal surface of tail closely grooved.

Reproductive Anatomy

Ovotestis has two clumps of finger-like alveoli, each clump c. 0.9 x 0.7 mm. Hermaphrodite duct proximally very slender, then gradually becoming distended to form a seminal vesicle (2.7 mm long) before narrowing and bending back sharply to terminate in the carrefour, with talon, embedded in the albumen gland. Talon spherical, c. 0.03 mm in diameter. Albumen gland ovoid, of variable size, 2.3 mm long in one dissected specimen. Spermooviduct (4.0 mm long) proximally cylindrical, distally distended, elongate ovoid, with narrow band of prostatic alveoli along its whole length. Free oviduct short (0.6 mm x 0.15 mm), increasing in width towards junction with spermathecal duct and vagina. Spermathecal duct with very broad base, gradually reducing to moderately slender tube terminating in round sac (0.7 mm diameter) resting against albumen gland. Vagina rather long (1.4 mm long), gradually reducing in width towards atrium. Vas deferens of uniform width throughout, passing through angle between vagina and penis close to atrium, to enter the penis apically adjacent to the retractor muscle. Retractor muscle has short, thick, circular, fleshy stalk, arising from diaphragm membrane half way along the pallial cavity close to the columellar muscle. Penis large, broadest at proximal end, gradually tapering to distal entry to atrium. Inner surface of proximal two thirds of penis essentially covered by short, stout papillae, that are slightly more elongated in the area around the vas deferens entry; papillae generally lacking in distal penis. One or more longitudinal depressions evident externally as darker zone(s) in the proximal penis correspond with an internal bridge between opposing walls, resulting with bifurcation of the penial lumen towards its proximal apex. Distal, tubular section of the penis, in some specimens, possesses a distended section.

Other Anatomy

Pallial cavity (8 mm long) has speckled black and white pigment on outer membrane. Kidney with a large pericardial lobe (3.6 mm long) and weak, acutely triangular rectal lobe. Ureter running along anterior face of the kidney and along hindgut to empty through respiratory pore. Wall of pallial cavity easily visible between two arms of ureter. Heart (1.4 mm long) slightly recessed into the outer wall of kidney pericardial lobe. Mantle collar 1.7 mm wide. Oesophagus, and the two salivary ducts, emerge from the roof of the buccal mass slightly forward of median dorsal point.

REMARKS

Six specimens were dissected, three each from the South and North Islands. Although Cumber (1961) noted differences between shells sourced from North and South Island localities, I could detect little difference in anatomy. Terminal genitalia in the South Island specimens dissected tended to be larger, though the shells were smaller. I have not followed up shell differences in this paper. See Table 4 for measurements.

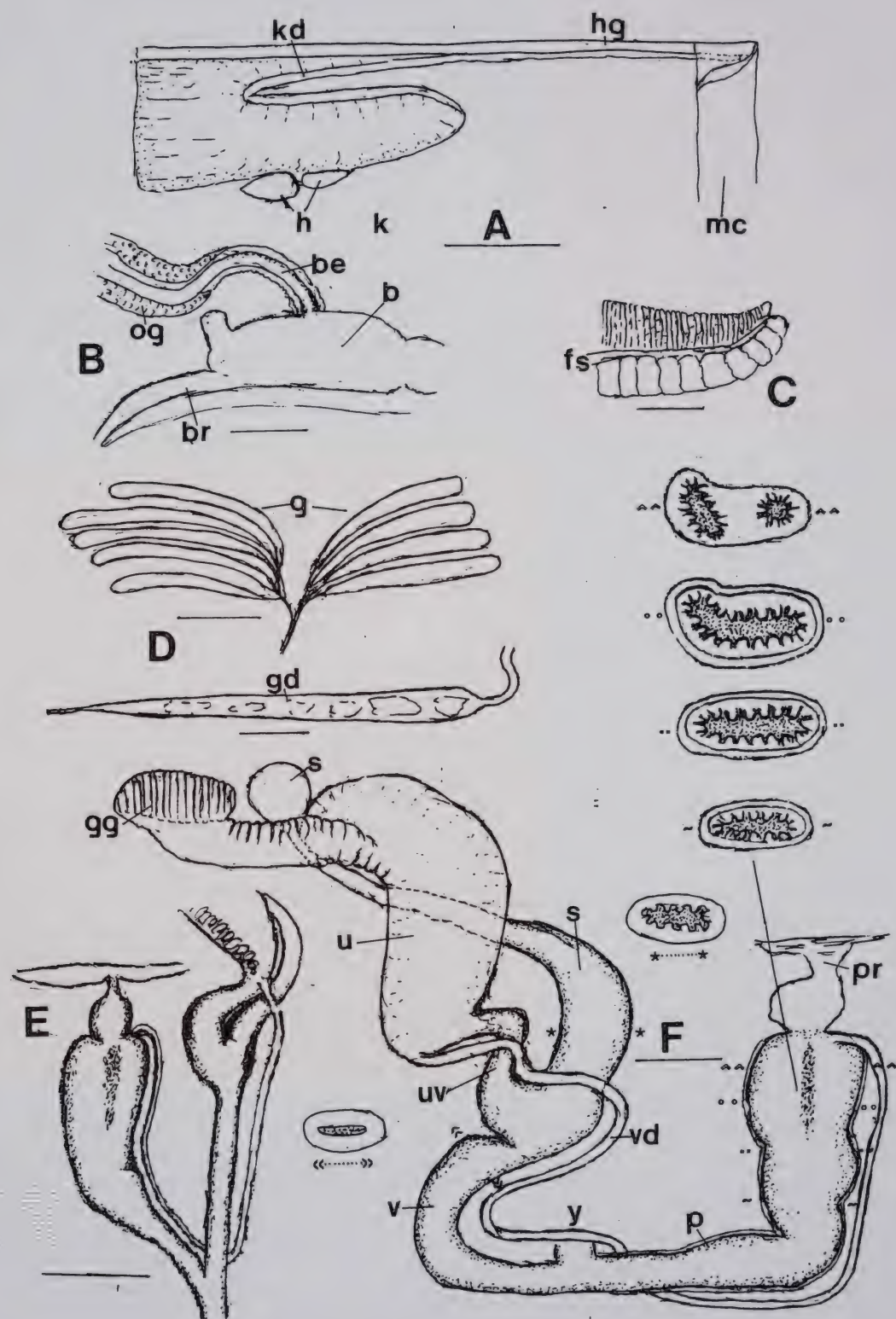


Table 4. Structural features of the shell of *Phenacohelix lucetta* (Hutton, 1884) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	Pelorus Sound	5.1	2.8	5.0	1.0	0.9	1.1	46	87
2	Pelorus Sound	4.8	2.5	4.8	1.1	0.9	1.0	35	78
3	Havelock	5.7	3.9	5.3	1.0	0.9	1.0	35	76
4	Wainuiomata	6.6	4.0	5.1	1.4	1.1	2.2	35	76
5	Rimutaka S.F.	5.6	3.2	5.0	1.2	1.0	1.0	30	75
6	Taihape	7.3	4.5	4.8	1.1	1.1	1.5	43	92

1, 2. AK151515, P26 752147, J.F. Goulstone 14/2/96. 3. AK151408, P27 739916, J.F. Goulstone 15/2/96. 4. AK155518, R27 734909 100 m, J.F. Goulstone 17/10/98. 5. AK155516, R27712824 100 m, J.F. Goulstone 17/10/98. 6. AK155638, T21 498665 396 m, P.C. Mayhill 1/12/98.

DISTRIBUTION AND HABITAT

Phenacohelix lucetta reaches its northern limit in coastal Bay of Plenty, North Island, and extends southward to the Marlborough Sounds and Nelson areas in the South Island. It is commonly found with *Charopa coma*, particularly under loose bark on fallen logs, or under logs or branches on the ground. It was found in large numbers, together with *Charopa coma*, under flax (*Phormium tenax*) and tree fern (*Cyathea* or *Dicksonia* spp.) at the Belmont Regional Park in Wellington (Hazelwood, Marston & Roscoe 24/5/99, AK-L22226).

Phenacohelix mahlfeldae n. sp.

Figs 6, 12

Phenacohelix pilula: Suter (1913), Cumber (1961) and Powell (1979); not of Reeve (1852).

ETYMOLOGY

Named for Karin Mahlfeld.

DESCRIPTION

Shell

Small (3.2 mm x 2.6 mm), globose, perforate, four and a half whorls, final whorl 0.7 mm wide. Protoconch 0.7 mm wide, 1.5 whorls, with fine pits and ridges. Aperture 0.6 of shell height. Teleoconch whorls with close, strong, rounded, primary axials, 40 on first whorl, 72 on last. Axials angled backwards from suture but quickly straightening and only slightly undulating

Fig. 5 (opposite). Anatomy of *Phenacohelix lucetta* (Hutton). Scale lines = 1 mm (A, E) or 0.5 mm (B, C, D, F). A-D, F. AK15151, Pelorus Sound. E. AK155638, Taihape. A. Pallial organs, ventral view. B. Position of oesophagus entering buccal mass. C. Posterior portion of foot. D. Ovotestis and expanded portion of hermaphrodite duct. E. Terminal genitalia. F. Reproductive organs. For key to abbreviations, see Fig. 1.

over perimeter into umbilicus. Interstices between primary axials (up to 0.1 mm wide) have up to 12 fine secondary axials. Whole teleoconch surface has microscopic spiral lirae. Umbilicus narrow (0.2 mm). Shell strongly coloured with bands and zigzags of reddish brown 5YR/4/4, on background of very pale brown 10YR/8/2. Sometimes zigzags on base fused together to form solid ring of reddish brown around umbilicus.

External Morphology

Whole animal, fully extended (less ommatophores), 4.7 mm long. Colour white, with a light grey strip along mantle collar and around respiratory pore. Ommataphoral retractor muscles light grey. Foot margin strongly crenellated, as is narrow space between two pedal grooves. Tail with shallow foss. Dorsal aspect of tail immediately behind mantle (0.6 mm) with shallow, transverse grooves, but posterior 0.4 mm becomes strongly crenellated.

Reproductive Anatomy

Ovotestis embedded in digestive gland, comprising two clumps of 3-4 long, finger-like alveoli, each 0.32 mm long. Hermaphrodite duct initially very slender, then expands 3-4-fold and becomes convoluted for almost whole length of stomach against which it rests. Crossing the lower reaches of the oesophagus, the hermaphrodite duct abruptly reduces in diameter and enters albumen gland. Details of carrefour and talon were not determined. Albumen gland (1.6 mm long) consists of very closely packed, small alveoli. Spermooviduct (1.75 mm long) ovoid, coarse prostatic alveoli in proximal half. Free oviduct (1.1 mm long) a thick, stout tube. Spermathecal duct narrow at origin, but expands rapidly into ovoid section whose lumen is reduced to a narrow Y-shaped gap by three broad, longitudinal ridges. Spermathecal duct then tapering, but still substantial, to reach a spherical sac (0.4 mm diameter) that rests against the albumen gland. Vagina very short in young specimen, absent in older one. Vas deferens arises from distal spermooviduct as moderately wide tube, then abruptly becomes slender to pass forward through angle between free oviduct and penis, to enter the epiphallus. Epiphallus 1.9 mm long, tubular, of uniform width throughout, thin-walled, opening slightly below the penial apex. Penis 2 mm long, elongated, pear shaped proximally, then simple short tube, distally, leading to atrium. Lumen of penis evidently smooth except for a large, oval block of fused, pillar-like pilasters protruding from wall in lower proximal section; in younger specimens the individual pilasters were not visible. Penis retractor muscle arising from the diaphragm at base of the kidney.

Other Anatomy

Pallial cavity 4.7 mm long, with a mixture of black and white pigment spots on the upper membrane. Kidney has large pericardial lobe (2.3 mm long), with heart (0.8 mm long) embedded in its right, somewhat crenellated margin; rectal lobe weakly developed, rounded. Ureter arises near anterior tip of kidney pericardial lobe, passes along anterior face of that lobe, turns forward along short rectal lobe, and follows hindgut to open through respiratory pore. Roof of pallial cavity visible between two arms of ureter. Stomach (2.5 mm long) has many strands of stringy

Fig. 6 (opposite). Shell and anatomy of *Phenacohelix mahlfeldae* n. sp. Scale lines = 1 mm (A-C, F, H) or 0.5 mm (D, E, G). A. Shell of holotype, AK73174. B. Shell showing band of red on ventral surface. C. Pallial organs, ventral view. D. Posterior part of foot. E. Reproductive anatomy. F. Hermaphrodite gland and duct. G. Part of terminal reproductive anatomy. H. Anterior of foot with pedal ganglia and pedal mucous gland. For key to abbreviations, see Fig. 1.

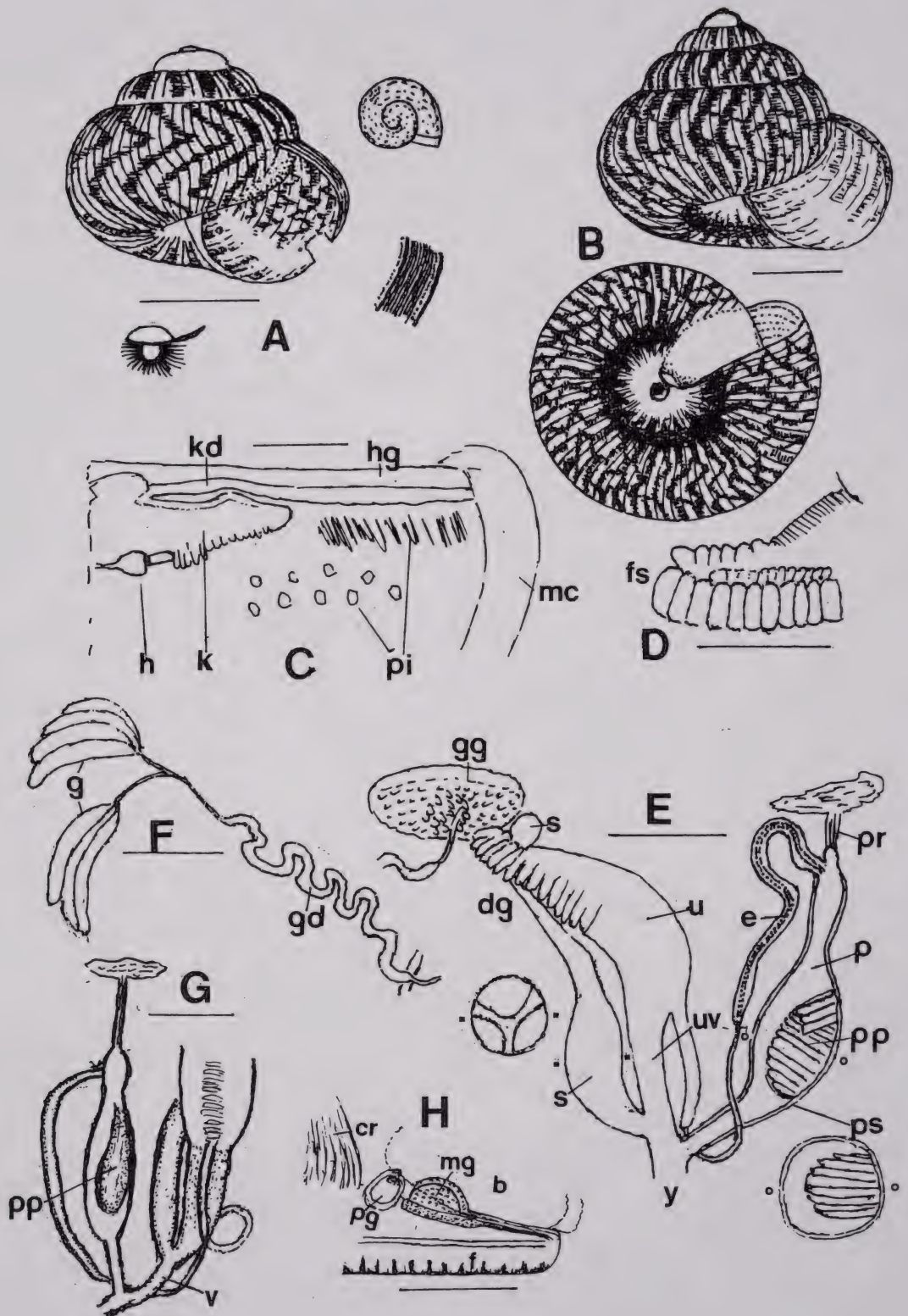


Table 5. Structural features of the shell of *Phenacohelix mahlfeldae* n. sp. based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	Tahakopa Sc. Res.	3.2	2.6	4.5	0.7	0.7	0.2	40	72
2	Tahakopa Sc. Res.	3.0	2.5	4.5	0.7	0.7	0.2	37	68

1. AK155159. 2. AK155654. Both Catlins, South Otago, G47 295005 10 m, P.C. Mayhill 1/4/98.

white pigment over surface. The pedal ganglia, lying beneath the buccal mass, each have a brightly white statocyst on the dorsal surface. Just forward of the pedal ganglia, two mucous glands empty below the mouth via small ducts.

REMARKS

The shell and anatomical descriptions given above are for the two dissected specimens, from Tahakopa Scenic Reserve, South Otago (Table 5). Further material from this site, suitable as types, was not available. A shell specimen from Dolomore Park, Southland, was selected as the holotype. Despite the geographic distance from Tahakopa, this choice seemed preferable to using the plentiful but as yet anatomically unknown Stewart Island material.

Although the shell of *P. mahlfeldae* n. sp. looks superficially like *P. pilula*, closer inspection reveals many differences. For example, *P. mahlfeldae* possess a smaller, more globose shell, which is more highly coloured, and with different protoconch sculpture. This is an uncommon snail in the south of the South Island but is more abundant on Stewart Island. *P. mahlfeldae* is well represented in subfossil deposits on Native Island.

TYPE LOCALITY

Southland, Croydon Bush, Dolomore Park F45 871527 210 m.

HOLOTYPE

AK73174, 2.3 mm x 1.9 mm, P.C. Mayhill 1/1/94. Other shell dimensions: protoconch 0.6 mm; last whorl 0.6 mm; aperture height 1.2 mm; umbilicus 0.2 mm; primary axials on first teleconch whorl 30, on final whorl 46.

PARATYPES

AK 73175 (4) Hokonui Range, Croydon Bush, kahikatea litter, F45 910527 J.F. Goulstone 22/2/95. MONZ 127645 (1) Purakaunui Falls Sc. Res. G47 456045 110 m K. Mahlfeld and P.C. Mayhill 12/4/98.

OTHER MATERIAL EXAMINED

SUBFOSSIL: Port Craig, Sandhill Point C46 721243, F.J. Brook 15/12/87, AK96709. Native Is., Stewart Is. E48, L. Fitzgerald 1/1/69, AK82998, E48, J.F. Goulstone 1/1/74, AK150170.

RECENT: Diamond Lake F40 897120 400 m, P.C. Mayhill 1/1/96, AK155924. Whakatipu, Bobs Cove F41 578609 360, P.C. Mayhill 1/1/89, AK155720. Kingston, Te Kea Haka Reserve F42 738335, J.F. Goulstone 9/3/98, AK154790; F42 746347 460 m, P.C. Mayhill 1/1/89, AK155704. Wye Creek F42 774577 420 m, P.C. Mayhill 1/6/89, AK155940. Te Anau, Brod Bay D43 928205, J.F. Goulstone

1/1/76, AK83016. **Blue Mountains, Black Gully** G44 265731, J.F. Goulstone 21/2/95, AK96544. **Taieri Gorge** I44 956089, J.F. Goulstone 1/1/91, AK155653. **Blue Mountains, Glenburnie Scenic Reserve** G45 213585, J.F. Goulstone 12/2/95, AK97007. **Waiau River, Big Totara Reserve** D45 937687, J.F. Goulstone 26/2/95, AK97029. **Clifden** D45 999494, J.F. Goulstone 25/2/95, AK96593. **Tapanui, Whisky Gully** G45 225657, P.C. Mayhill 1/1/99, AK155690. **Pahia Hill Scenic Reserve** D46 025187, J.F. Goulstone 20/2/95, AK150379. **Forest Hill** E46 573354 180 m, P.C. Mayhill 1/9/83, AK155938, E46 574354 180 m, P.C. Mayhill 1/9/83, AK155939. **Egremont Rd.** F46 073185 320 m, P.C. Mayhill 1/1/94, AK155941. **Catlins, Samsons Hill** G47 253954 200 m, P.C. Mayhill 1/1/94, AK155248. **Halfmoon Bay** E48, E. Smith 1/5/49, AK83012. **Fishermens Rock Pt.** E48 407573, N. Douglas 1/5/71, AK153199. **Road to Golden Bay** E48, E. Smith, AK82995. **Behind woolshed** E48, E. Smith 1/6/49, AK82996. **Ulva Is.** E 48, A.E. Brookes, AK82981. **Maori Bay, east end** E48 353612, J.F. Goulstone 1/1/74, AK150166. **Lords River** E49 401350 20 m, N. Douglas 10/5/71, AK153189.

DISTRIBUTION AND HABITAT

The species is present in South Otago, Southland and Stewart Island. The two Catlin specimens dissected were found in bush on the ground, crawling on sticks 2-3 cm in diameter. The Whiskey Gully specimen was collected from under a stone.

Phenacohelix perplexa (Murdoch, 1897)

Figs 7, 12

DESCRIPTION

External Morphology

Foot sole thin, white, its margin weakly crenellated and surmounted by two pedal grooves. Posterior section of sole smooth. Dorsal surface of tail smooth, flecked with grey-black, tip of tail white.

Reproductive Anatomy

Ovotestis has two crowded clumps of finger-like alveoli, each 1 mm wide, embedded in digestive gland close to stomach apex. Hermaphrodite duct initially very slender, but for most of its length (2.5 mm) distended as seminal vesicle (0.3 mm wide), before reducing in diameter to terminate in the carrefour embedded in the albumen gland. Talon not detected. Albumen gland variable in size, but generally small (up to 1.2 mm); consisting of very small, crowded alveoli. Spermooviduct (2.9 mm long) tubular, narrow but for weak globular dilation in middle section. Free oviduct (1.3 mm long) slightly narrower tube than distal section of the spermooviduct. Spermathecal duct narrowed at opening to free oviduct, but expanding three-fold in width to produce a prominent, ovoid basal section with low, wavy internal ridges, then narrowing abruptly to run to large, ovoid sac (up to 1.4 mm long) that rests between albumen gland and columellar muscle. Vagina short (0.4 mm long), about same width as free oviduct. Vas deferens slender throughout passage through angle of vagina and penis close to the male genitalia. Epiphallus short, stout (0.6 mm long x 0.15 mm wide), slightly arched, opening at apex of the penis adjacent to the penial retractor. Penis consists of a small upper or proximal chamber, a large middle chamber which can be globular or produced laterally as an indistinct caecum, and a distal tube, reducing to same width as vagina where they meet in atrium. Internally, penis with short papilla, produced initially as an array around opening of the epiphallus, then produced into low ridges and folds in the proximal and middle chambers. Wall of middle chamber greatly thickened as a large, bulky pilaster, cover with papillae, and extending into the caecal pocket. Distal penis initially possesses several low ridges. Penial retractor muscle is anchored to the diaphragm, close to base of the kidney.

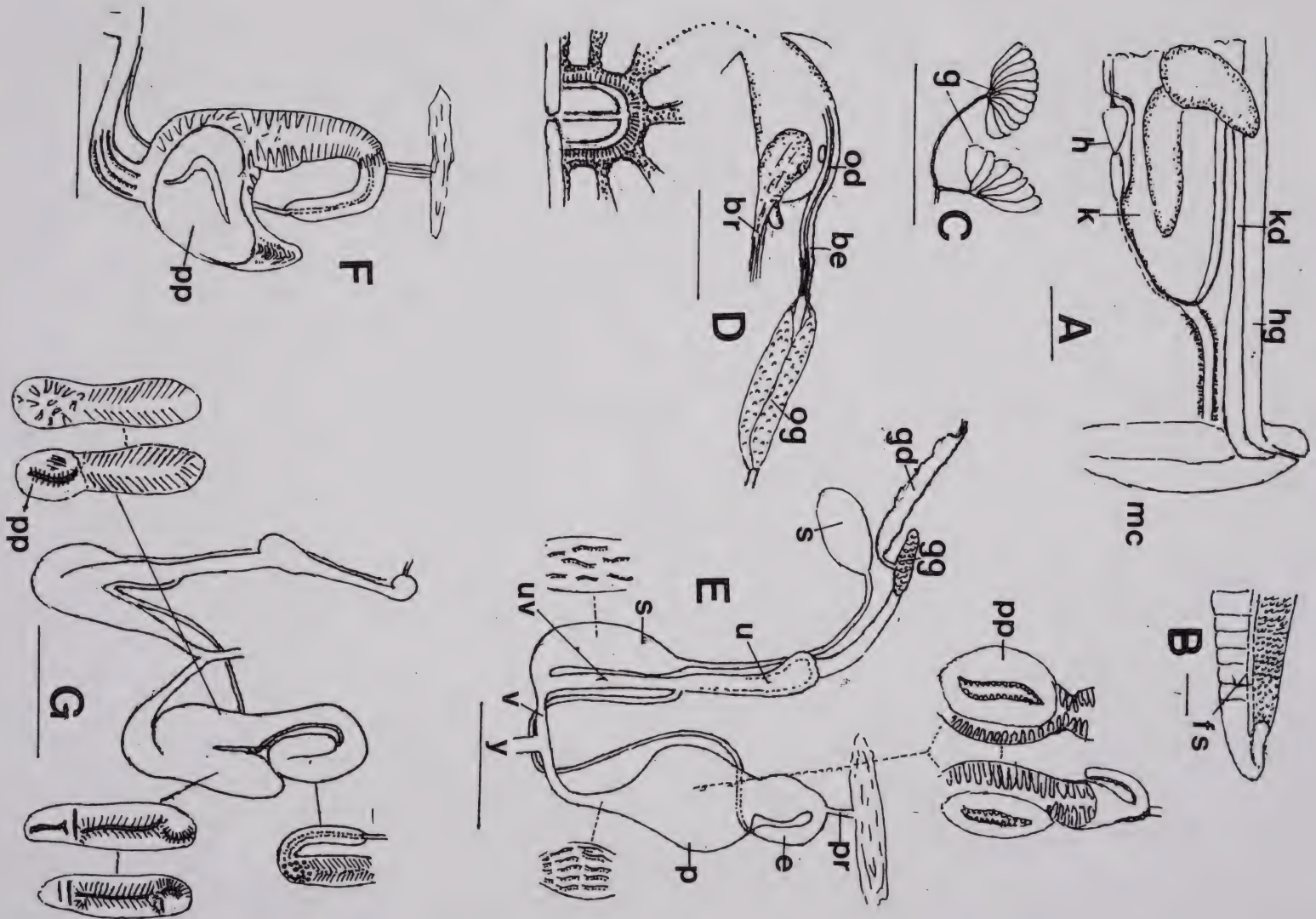


Table 6. Structural features of the shell of *Phenacohelix perplexa* (Murdoch, 1897) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality	Shell parameters							
	1	2	3	4	5	6	7	8
1 Waenga	6.3	4.3	4.8	1.3	1.8	0.9	37	81
2 Papatea	5.6	4.2	4.5	1.3	1.6	0.7	38	83
3 Gordon Park	6.9	4.2	4.5	1.3	1.6	1.2	46	142
4 Gordon Park	6.9	4.2	4.3	1.3	1.8	1.1	40	121

1. AK154596, Y14 652913 140 m, G.M. Barker 16/9/92. 2. AK154589, Y14 385806 100 m, G.M. Barker 14/9/92. 3, 4. AK155523, R22 895415 30 m, J.F. Goulstone 15/10/98.

Other Anatomy

Pallial cavity 6.2 mm long, with much black pigment over the outer membrane. This black pigmentation also extending over the rest of the animal. Mantle collar 1.2 mm wide. Kidney large (4.1 mm long). Ureter passes from apex of the kidney along anterior face of the pericardial lobe, then turns forward along face of rectal lobe and thence following hindgut to open through the respiratory pore. Roof of pallial cavity visible between two arms of the ureter. Heart (1.5 mm long) recessed into kidney, with main pulmonary vein prominent in anterior of the pallial cavity. Oesophagus, flanked by the salivary ducts, enters roof of the buccal mass near its median, dorsal point. Buccal retractor muscle attachment prominent on posterior half of buccal mass. Pedal ganglia situated under the buccal mass, each with a statocyst, as glistening white spot, on their dorsal surface.

REMARKS

Four specimens were dissected, two from East Cape, two from Wanganui. One specimen, which had up to 1.1 mm of jelly-like material along the proximal and middle sections of the spermoviduct, also had the distal section of the spermoviduct somewhat enlarged and free oviduct shorter and wider. In only one specimen was there evidence of prostatic alveoli on the proximal spermoviduct, and they were very weakly developed. The penis of all dissected specimens was essentially the same structure but varied in shape. The least sexually mature specimen had the most pronounced penial caecum, with the rudiments of a pilaster. In the most developed specimen the caecum was barely discernable. It may be that the younger snails start with a fully developed penial caecum, and that this structure is partly or wholly lost with age. I did not observe any differences between the material from East Cape and Wanganui. Table 6 gives measurements for this species.

Fig. 7 (opposite). Anatomy of *Phenacohelix perplexa* (Murdoch). Scale lines = 1 mm. A-E. AK15523, Gordon Park. F. AK154589, Papatea. G. AK154596, Waenga. A. Pallial organs, ventral view. B. Posterior portion of foot. C. Ovotestis. D. Buccal mass, showing oesophagus entry and enlarged view of mouth parts. E. Reproductive organs. F. Penis from another specimen showing enlarged internal pilaster. G. Reproductive organs from a younger specimen showing pilaster in early stages. For key to abbreviations, see Fig. 1.

DISTRIBUTION AND HABITAT

Specimens held in the Auckland Museum suggest that *P. perplexa* has a disjunct distribution, being confined to around East Cape and around Wanganui. However, material in the Museum of New Zealand includes specimens from intermediate localities (F.M. Climo pers. comm.), pointing to a more generalised distribution in the central North Island. The specimens I collected from around Wanganui were all on the undersides of logs on the ground.

Phenacohelix pilula (Reeve, 1852)

Figs 8, 12

DESCRIPTION

External Morphology

Foot margin weakly but finely crenellated. Two pedal grooves, with crenellations between them, end posteriorly in a caudal foss surmounted by a caudal horn. Dorsal surface of tail grey, with shallow segmented grooves.

Reproductive Anatomy

Ovotestis (1.2 mm x 0.9 mm) consists of two clumps of finger-like alveoli embedded in digestive gland tissue. Hermaphrodite duct initially slender, but soon becomes distended to a sickle-shaped seminal vesicle (0.3 mm wide), then reduces to a short, slender section to terminate in the carrefour on ventral aspect of the albumen gland. Talon spherical, on a short stalk. Albumen gland (up to 2.3 mm long) ovoid, consisting of dense, minute alveoli. Spermooviduct oblong (2.0 mm long x 0.6 wide), with prostatic alveoli along whole length but more concentrated and prominent proximally. Free oviduct variable in length and width, proximal half generally narrower (0.15 mm wide) than distal half, the latter tends to be bulbous; lumen uniform diameter throughout its length. Spermathecal duct broad at origin in oviduct, usually wider than distal section of free oviduct, but tapers steadily to terminate in an oval sac (0.4 mm long) buried in prostatic alveoli close to the albumen gland; base of duct has internally several flap-like ridges leading from vagina. Vagina (1.0 mm long) tapers from union with spermathecal duct and oviduct, towards atrium, but is sometimes distended medially. Vas deferens slender throughout, enters penis a little below the latter's apex. Penial retractor muscle has its origin in the diaphragm near the base of the kidney, and inserts on the apex of the penis. Penis (3.4 mm long) comprises two chambers, separated by a restriction of the outer wall, and a distal tube of variable length leading to the atrium. The proximal chamber has thick walls, internally covered with crowded papillae, leaving only a small central passage. The second penial chamber is similarly lined with papillae, for a large part forming low ridges orientated towards the opening of penial caecum arising from the upper lateral wall. Penial caecum wide (0.3 mm),

Fig. 8 (opposite). Shell and anatomy of *Phenacohelix pilula* (Reeve). Scale lines = 1 mm (A, B, E-G) or 0.5 mm (C, D). A. Reconstructed drawing taken from photo of holotype, scale produced from Suter's type measurements. B. Shell from Port Waikato, AK155671. C. Reproductive anatomy of specimen from Mill Bay, Coromandel; other cross-section of proximal penis from a similar specimen from same location. D. Ovotestis and hermaphrodite duct. E. Pallial organs, ventral view. F. Reproductive anatomy of a younger specimen from Port Waikato. G. Reproductive anatomy of a specimen from Mimiwhangara with lumen features changed in distal chamber of penis, free oviduct and base of spermathecal duct. For key to abbreviations, see Fig. 1.

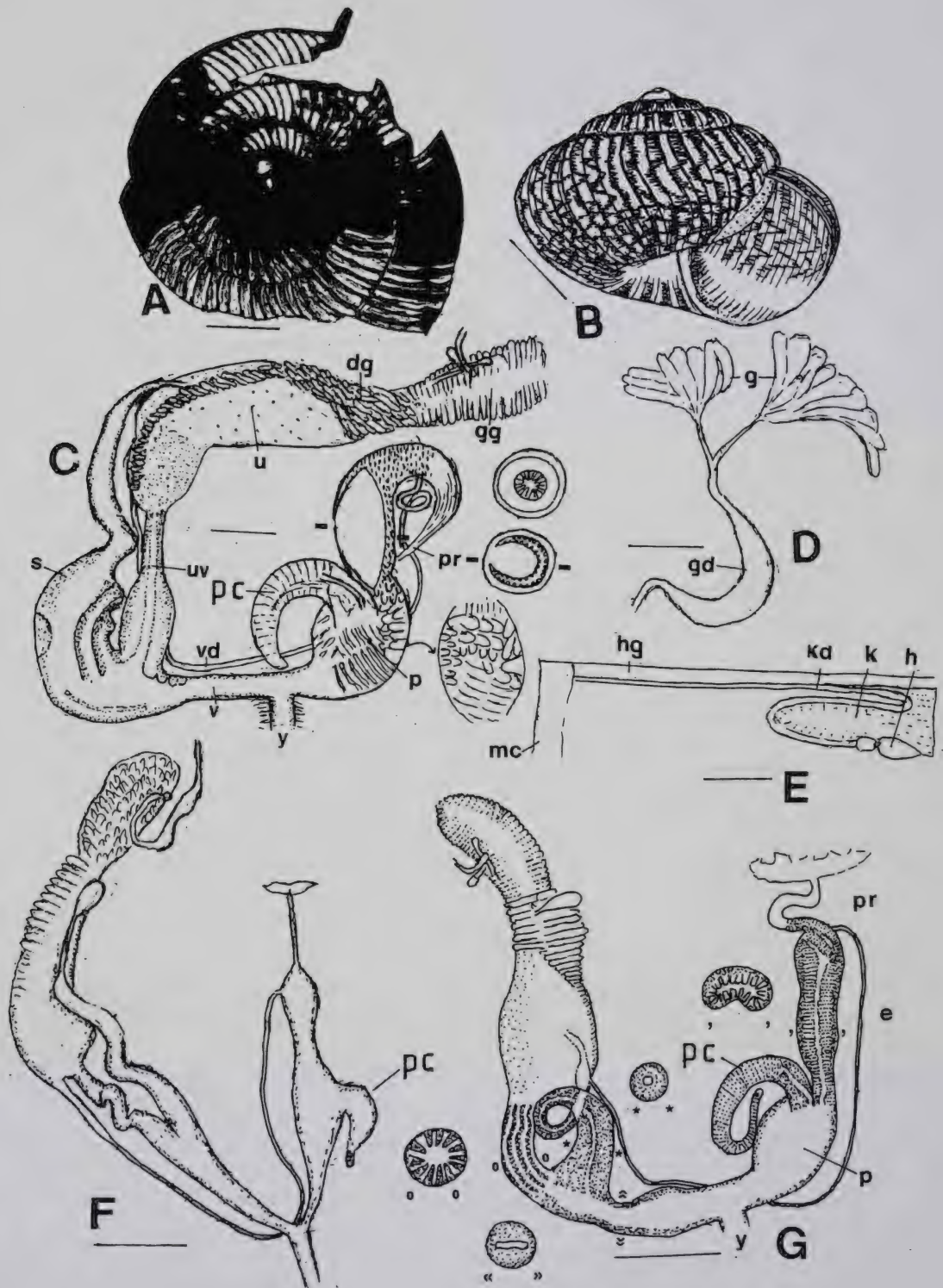


Table 7. Structural features of the shell of *Phenacohelix pilula* (Reeve, 1852) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	Whangaroa	4.2	3.4	4.8	0.8	0.9	0.3	34	72
2	Waiwera	3.2	2.7	4.3	0.7	0.5	0.2	36	66
3	Umupia Reg Park	2.9	2.4	4.0	0.7	0.8	0.2	36	58
4	Mill Creek	3.1	2.1	3.8	0.5	0.9	0.3		
5	Mill Creek	3.1	2.1	3.8	0.9	0.9	0.3		
6	Tuahu Tr., Kaimai	5.7	3.6	5.0	0.9	1.5	1.0	40	94
7	Lake Tarawera	5.7	3.8	4.8	1.5	1.6	0.9	40	100
8	Port Waikato	3.7	2.5	4.2	0.7	0.9	0.3	31	66

1. AK155211, P04 788826, B.F. Hazelwood 24/5/98. 2. AK96820, J.F. Goulstone 14/4/95. 3. AK154012, S11 955747, J.F. Goulstone 26/11/95. 4, 5. AK80615, T11 766473 J.F. Goulstone 1/4/83. 6. AK154567, T14 624961 400 m, P.C. Mayhill 1/4/97. 7. AK154622, U16 056273 304 m, G.M. Barker 1/1/80. 8. AK155250, R13 684277 60 m, B.F. Hazelwood 22/6/98.

thick-walled and with very narrow opening where it joins penis, but reduces to a more saccular structure, with blunt, often recurved, tip and thin, transparent walls strengthened by close concentric rings.

Other Anatomy

Pallial cavity 6 mm long, with heavy black pigment on roof. Kidney has long, ovoid pericardial lobe (2.5 mm long) with heart (0.8 mm long) recessed, and a weak, slender rectal lobe. Ureter starts at kidney apex, passes along anterior face of pericardial and rectal lobes and then along hindgut to open through respiratory pore. Roof of pallial cavity can be seen between adjacent arms of the ureter. Oesophagus, with flanking salivary ducts, joins roof of buccal mass near its median dorsal point. Glistening white statocysts are visible on the dorsal surface of the pedal ganglia situated under the buccal mass.

REMARKS

Cumber (1961) evidently only studied true *P. pilula*, collected by him from the north of the South Island. Although he published Suter's distribution list and included the southern South Island records in a distribution map, he may never have seen the southern material. It is thus possible that Cumber's southern records of '*pilula*' actually pertain to *P. mabelfeldae*.

Eight specimens of *P. pilula* were dissected in the present study (Table 7). A specimen from Mill Bay, Whitianga, had what appeared to be a large, fleshy pilaster in the proximal penial chamber. However, the second specimen for that locality had thick walls and a circular central channel (Fig. 8C). A specimen from Mimiwhangata had the lower chamber of the penis devoid of any internal papillae, the free oviduct with many internal, plate-like ridges, and with the base of the spermathecal duct thick-walled with a simple, narrow lumen.

DISTRIBUTION AND HABITAT

Phenacohelix pilula is wide ranging in the North Island, although absent from the Far North. It

has been collected frequently in the Nelson and Marlborough Sounds areas, and more sparingly in Canterbury and Otago. *P. pilula* is evidently absent from the West Coast or Southland regions. In the Taieri Gorge, *P. pilula* is sympatric with *P. mabelfeldae* (AK83003). Live specimens are most often collected from forest leaf litter, but have also been collected as they crawl on the fronds of low-growing ferns.

Phenacobelix ponsonbyi (Suter, 1897)

Figs 9, 12

DESCRIPTION

Shell

Small (5.5 mm x 3.7 mm), depressed globose. Whorls, four and a half in mature animals, are flatly rounded, final whorl 1.5 mm wide. Aperture 2.4 mm high x 2.8 mm wide. Protoconch 0.9 mm wide, of 1.1 whorls, with close, spiral lirae. Teleoconch whorls have closely-spaced primary axials, arising from a shallow suture and sloping gently away from direction of shell growth on dorsal surface, sinuous on ventral surface into the umbilicus. Axials numbering 43 on first teleoconch whorl, and 114 on final whorl, are each slightly rounded at apex. Interstices have fine, crowded secondary axials (up to 14). Microscopic spiral sculpture hardly noticeable (up to 60x magnification). Umbilicus 1.4 mm wide. Colour is very pale brown 10YR/83, superimposed with reddish brown 5YR/4/4 flashes and zigzags.

External Morphology

Foot margin crenellated, with two pedal grooves above that terminate posteriorly in a slight depression at the tail. Narrow space between pedal grooves also crenellated. Dorsal surface of tail has close shallow horizontal grooves up to mantle collar.

Reproductive Anatomy

Ovotestis, embedded within the digestive gland tissue, comprises two pyramid-like clusters of alveoli. Hermaphrodite duct initially very slender, then expands in diameter four fold to run for 2.3 mm as the seminal vesicle, before again reducing to enter carrefour partially embedded in albumen gland. Carrefour complex carries an oblong talon, 0.2 mm long. Albumen gland (2.3 mm long) comprises closely crowded alveoli, narrows (0.3 mm wide) where it joins spermoviduct. Spermoviduct elongate, oval, with thick finger-like prostatic alveoli as band along proximal two thirds. Free oviduct a long tube (1.6 mm long x 0.3 mm wide), expanding slightly at entry into vagina, where its lumen bears longitudinal folds. Spermathecal duct expands from origin into ovoid basal section (base 1.4 mm long), then reduces to fine tube that terminates in an oval sac (0.5 mm long) resting against albumen gland; lumen of spermathecal base with longitudinal ridges. Vagina short, slightly globular, with internal, crowded, fine circular ridges. Vas deferens arises from distal spermoviduct as tube of similar width and length as free oviduct, but then abruptly reduces to fine tube passing through angle of penis and vagina close to atrium and enters penis somewhat below apex. Epiphallus evidently absent. Penis retractor muscle arises from diaphragm membrane about half way along pallial cavity, attached to penis apically. Penis (2.8 mm long) comprises three sections: a bulky, weakly ovoid proximal section (1.1 mm wide); a bulky, weakly ovoid middle section; and a narrow, short, tapering distal section (0.4 mm wide) opening to the atrium—proximal and middle sections often separated by slight constriction. Internally the proximal penis is completely covered in short papillae, the middle section possesses a number of low, horizontal ridges, and the distal section is evidently

smooth. Opening to the upper part of the middle penial section, and curled towards the atrium, is a penial caecum, comprising essentially a thin-walled tube strengthened by concentric ridges, half the length of the penis, broadest where it joins the penis and reducing in width to terminate in narrow tail curled back on itself. A narrow orifice connects this organ with the penis.

Other Anatomy

Pallial cavity (5 mm long) has blotches of black and white pigment on its outer membrane. Kidney pericardial lobe large (2.3 mm long), with the pericardium (1.1 mm long) impressed into its outer wall. Rectal lobe rather small. Ureter passing from apex of pericardium lobe, along anterior face of the kidney, to angle with short rectal lobe, then following hindgut to exit through respiratory pore. A wide gap exists between the primary and secondary arms of the ureter. Oesophagus, and flanking salivary ducts, enter roof of buccal mass near median dorsal point. Pedal ganglia evidently fused, with glistening white statocysts on their dorsal surface.

REMARKS

The type locality of *Phenacohelix ponsonbyi* is the Mt Wellington lava fields, Auckland. The type locality has been virtually lost to urbanisation, with the area largely covered in houses and factories. No forest cover remains. At the time of writing (August 1998), B.F. Hazelwood could find only one empty *P. ponsonbyi* shell at R11 726758, where 20 years ago the species was still abundant. This site is to be developed as a quarry but is presently covered with exotic weeds and litter.

Cumber (1961) determined that the *P. ponsonbyi* (Suter) of most authors subsequent to Suter (1897) comprised two forms separable on shell characters. Cumber chose plesiotypes from the Waikato to more properly represent the dominant form. That dominant form is formally described in the present paper as *Phenacohelix hakarimata* n. sp. (see below).

I have redescribed the shell of *P. ponsonbyi* because Cumber's description encompasses the two species. The shell description and illustration given in the present paper are of a typical topotype specimen from the Mt Wellington lava fields (AK83085 R11 726758, Mrs D. Hole 29/8/76). The colour is taken from a fresh specimen. Cumber has adequately described the lectotype and I repeat his measurements below. The flatness of the dorsal surface with attendant shallow suture and raised protoconch, accelerated final whorl, wider umbilicus and slightly larger mature shells, distinguish *P. ponsonbyi* from *P. hakarimata* n. sp. I dissected five specimens, all from Auckland, the shell measurements of which are given in Table 8.

TYPE LOCALITY

Mt Wellington lava fields, Auckland.

LECTOTYPE

MONZ 125160, 5.25 mm x 3 mm, umbilicus 0.9 mm, ribs on first teleoconch whorl 36, third teleoconch whorl 82. Measurements from Cumber (1961).

Fig. 9 (opposite). Shell and anatomy of *Phenacohelix ponsonbyi* (Suter). Scale lines = 1 mm. A. AK83085, Mt Wellington. B-E. AK155252, Cosseys Dam 1. A. Shell. B. Posterior portion of foot. C. Ovotestis and hermaphrodite duct. D. Pallial organs, ventral view. E. Reproductive organs. For key to abbreviations, see Fig. 1.

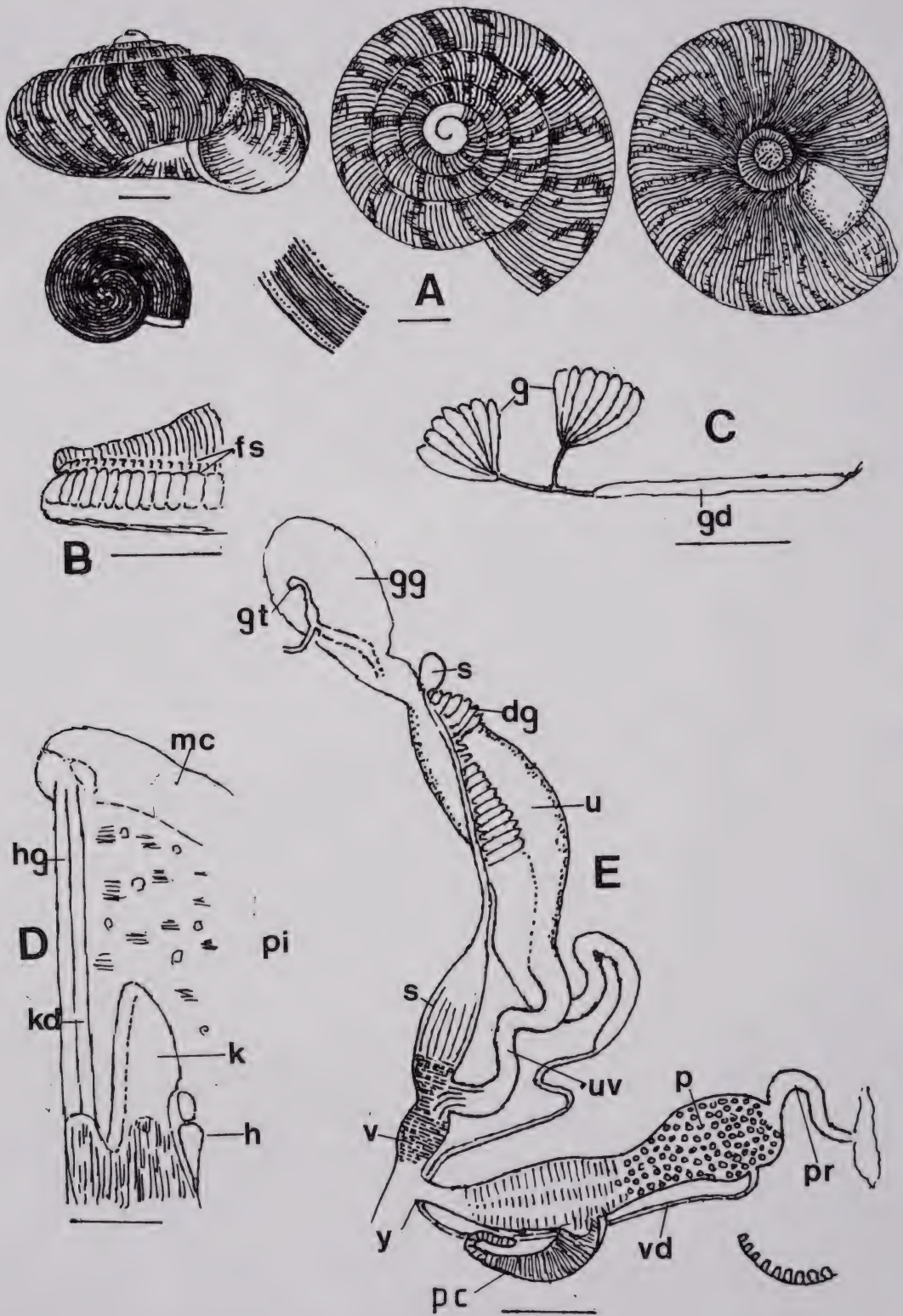


Table 8. Structural features of the shell of *Phenacobelix ponsonbyi* (Suter, 1897) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality		Shell parameters							
		1	2	3	4	5	6	7	8
1	Cosseys Dam	5.3	3.0	4.5	0.8	1.6	1.0	36	86
2	Cosseys Dam	5.2	3.1	4.3	0.9	1.5	0.9	36	89
3	Cosseys Dam	5.3	3.1	4.5	0.9	1.5	0.9	39	97
4	Twilight Rd.	5.6	3.6	4.5	0.9	1.6	1.0	38	83
5	Mangere Mountain	5.8	3.5	4.5	0.9	1.7	1.0	35	95

1, 2, 3. AK155252. 4. AK150852. 5. AK155338. All collected J.F. Goulstone.

PARALECTOTYPES

MONZ 125159 (2), from type locality.

OTHER MATERIAL EXAMINED

Waiwera, Puhoi Hill R10, A.W.B. Powell 5/4/47, AK83075. Muriwai, Korekore Pa Hill Q11, A.W.B. Powell 1925, AK83074. Government House R11 680792, J.F. Goulstone 17/11/95, AK150531. Clevedon, Twilight Rd. R11 898667, J.F. Goulstone 7/2/98. Mt Wellington lava fields R11 726759, J.F. Goulstone 1/1/76, AK155217, B.F. Hazelwood 1/8/98, AK155367; 726758, D. Hole 29/8/76, AK83085; J.F. Goulstone 1/12/85, AK83086. Mangere Mountain R11 692709 50 m, J.F. Goulstone 4/8/98, AK155341. Waiatarua R11, AK83073. Titirangi R11, 30/10/26, AK83080. Wiri stonefields R11 743632, J.F. Goulstone 1/11/87, AK83076. Hunua Gorge R12 868570, J.F. Goulstone 1/5/89, AK155220. Waiuku R12, W.H. Webster, AK83072. Cosseys Dam S12 974578 230m, J.F. Goulstone 1/3/83, AK83087, 21/6/98 AK155237, 29/6/98 AK155251; S12 975582 210 m, P.C. Mayhill 1/8/78, AK156105. Mt William S12 903414 200 m, P.C. Mayhill 1/8/81, AK156094. Mangatawhiri S12 029497 140 m, P.C. Mayhill 1/1/78, AK156118. Parakiwai T12 616327 60 m, P.C. Mayhill 1/11/82, AK154100; T12 535516 180 m, P.C. Mayhill 1/9/79, AK156080. Kaitarakihi T12 479467 420 m, P.C. Mayhill 1/2/94, AK156103. Waikaretu R13 665045 20 m, P.C. Mayhill 1/9/77, AK155501. Colebaker Ridge R13670235 200 m, P.C. Mayhill 1/6/83, AK155549. Tauhei Quarry S13 174075 60 m, P.C. Mayhill 1/3/79, AK156122. Four Brothers Scenic Reserve S14 927728, P.C. Mayhill 1/7/83, AK155539. Kawhia-Raglan R15 737508 60 m, P.C. Mayhill 1/11/79, AK155510. Maungakawa No. 1 T15 325686 200 m, P.C. Mayhill 1/3/85, AK155507. Pirongia State Forest Park R16 883388 360 m, P.C. Mayhill 1/10/83, AK155536. Waipuna Reserve R16 836113 396 m, G.M. Barker 29/3/77, AK154642. Waitomo S16, A.E. Brookes, AK83084; S16 945250 91 m, G.M. Barker 1/9/89, AK154636. Mangaokewa S16 996176 40 m, P.C. Mayhill 1/11/80, AK155418. Ruakuri S16 818249 260 m, P.C. Mayhill 1/5/84, AK155509. Whareorino R17 609078 340 m, P.C. Mayhill 1/3/83, AK155508. Aorangi Reserve R17 599819 60 m, P.C. Mayhill 1/3/78, AK155415. Awakino Gorge R17 595819 60 m, A. Eagle 1/11/81, AK155497. Pureora, Hurakia Block S17 246840, J.F. Goulstone 1/4/82, AK150400. Mt Messenger Q18 487554 200 m, P.C. Mayhill 1/10/80, AK155479. Mokau Scenic Reserve R18 546762 40 m, P.C. Mayhill 1/9/86, AK155485; R18 546763 40 m, P.C. Mayhill 1/5/87, AK155472. New Plymouth, Te Henui Walkway P19 046374, J.F. Goulstone 1/12/88, AK150058. New Plymouth P19 064331 80 m, P.C. Mayhill 1/4/87. New Plymouth, Brooklands P19 037867, J.F. Goulstone 1/12/88, AK97935. Wanganui, Bushy Park R22 752545 200 m, P.C. Mayhill 1/8/97, AK155491.

DISTRIBUTION AND HABITAT

Phenacohelix ponsonbyi s. str. evidently has a narrow geographic range and never seems to be abundant. Shells referable to *P. ponsonbyi* have been found in low numbers (usually one or two per locality) in western districts from Auckland to as far south as Wanganui, with the largest collection from a site at Aorangi Reserve (7 specimens). One site on the East Coast, at Parakiwai (P.C. Mayhill), has also been registered. At Cosseys Dam, Hunua Ranges, which is the best site I found for *P. ponsonbyi*, the gorge below the dam is rocky, a characteristic common to most of the sites where it is plentiful. Snails here were present inside the stalks of rotting tree fern fronds, under bark of rotting trunks and in fallen nikau fronds. At Mangere Mountain and Wiri, *P. ponsonbyi* was living among scoria rocks with a covering of *Muehlenbeckia*. At Government House, Mt Eden, the species was found living among rocks under a canopy of shrubs and trees replicating the environment at the now defunct type locality.

Phenacohelix tholoides (Suter, 1907)

Figs 10, 12

DESCRIPTION

External Morphology

Foot white, its margin weakly crenellated and with two closely-spaced pedal grooves ending in caudal foss at the posterior. Caudal horn present but not pronounced. Dorsal surface of tail grey, with close shallow grooves.

Reproductive Anatomy

Ovotestis comprising two clumps of finger-like alveoli (0.6 mm wide), embedded in digestive gland tissue close to stomach apex. Hermaphrodite duct proximal section (0.4 mm) very slender, but becomes distended to a seminal vesicle (0.1 mm diameter x 1.6 mm long) before tapering to terminate in the carrefour embedded in the ventral face of the albumen gland. Talon oblong (0.15 mm long). Albumen gland (up to 2 mm long) ovoid, placed in loop of intestine, consists of minute, closely-packed alveoli. Spermooviduct (2.7 mm long), cylindrical, uniformly broad but for narrow (0.2 mm) section where it arises from the albumen gland. Prostatic gland alveoli evident as a narrow strip along full length of the spermooviduct. Free oviduct (1.8 mm long) variable in width (1.5-2.0 mm). Spermathecal duct with bulbous basal region, tapering rapidly to a slender duct that follows spermooviduct and terminates in an oval sac resting against the albumen gland in the vicinity of the pericardium; epithelium of the spermathecal duct basal region produced as longitudinal flaps that extend to the centre of luminal cavity. Vagina short and stout (0.3 mm x 1.5 mm). Vas deferens short, uniformly slender, soon giving rise to the epiphallus that comprises an elongate, spindle-shaped proximal section and a slender, convoluted distal section. The proximal section of the epiphallus sometimes coils back upon itself, and is united to middle region of penis by connective tissue; this evidently occurs very early in formation of reproductive organs but does not persist when the genitalia are fully formed. Epiphallus inserting subapically on penis. Retractor muscle, attached to apex of penis, a short, tapered stalk fastened to diaphragm near base of the kidney. Penis proper (1.8 mm long) consists of two parts of roughly equal length. The proximal penis is an oval chamber upon a narrowed tubular extension leading to the distal penis. Internally this proximal section has small spinate papillae or "thorns" in the apical cavity, an extensive cluster of elongate pilasters around the verge formed by entry of the epiphallus and, in the main lumen, with numerous large spinate papillae and a longitudinal row of paired small, spinate papillae. This paired row of spinate papillae

runs into the junction with the distal penis. Distal section of penis cylindrical, with lumen lined with four broad, smooth, longitudinal folds. Penial caecum arising from lateral wall of penis proper, at junction of proximal and distal sections, its lower reaches a cylindrical to bulbous chamber whose wall possesses spinate papillae similar to that in the proximal penis proper. A large, hollow dart (0.4 mm long) arises from the thickened apical wall of the caecum to project into the lumen; the dart is evidently expendable and is sometimes absent or broken. The dart is continued external to the caecum by a elongate, thin-walled, striated, glandular tube, which scribes a looping round the penis and is fastened at its apex by connective tissue and muscle strands to the caecal wall near its point of origin. Caecum firmly bound to the lower reaches of the proximal penis by many layers of strong fibrous material.

Other Anatomy

Pallial cavity 7.7 mm long, with scattered spots of black and white pigment on the outer membrane. Kidney 3.0 mm long, dominated by strong pericardial lobe, with heart (1.3 mm long) recessed on outer margin, and with an indistinct rectal lobe. Ureter along anterior face of pericardial lobe from apex to junction with rectal lobe, then turning forward along hindgut to open through respiratory pore slightly behind anus. Adult specimens had no gap between the ureter arms. Oesophagus, and flanking salivary ducts, enter posterior extremity of the buccal mass. Statocysts gleaming white, visible on dorsal surface of the pedal ganglia that are located under the buccal mass.

REMARKS

Ten specimens of *Phenacohelix tholoides* (Suter, 1907) were fully dissected (Table 9). An animal extracted from a shell less than 4 mm in diameter proved to be reproductively immature, but some additional animals extracted from shells over 4 mm were also under-developed. A specimen from Ngahau Bay (AK154067), of shell size 3 mm and without discernible genitalia, nevertheless had a very well developed hermaphrodite duct. A further specimen from Ngahau Bay (Fig. 10H) was without the bulbous body of the penial caecum. Southern specimens were collected from April to August and were sexually fully mature. Te Paki specimens were collected in November and December and were immature, suggesting a phenological cycle. Clearly a larger sample needs to be examined to establish the reproductive phenology of the species. I have illustrated some undeveloped penial lumina: Fig. 10F = specimen 3 in Table 9, Fig. 10G = specimen 5 in Table 9.

OTHER MATERIAL EXAMINED

SUBFOSSIL: Many shells from several well documented sites have been recovered from the sandhills of Cape Maria van Diemen, Herangi Hill and behind Te Werahi Beach by F.J. Brook and C. Laurenson, 1993-97. One central site, for example, is at M02 800473. Because of their proximity I list only registration numbers. AK85548, AK89363, AK91678, AK91680, AK91693, AK91711, AK91718, AK91754, AK91771, AK91781, AK91792, AK91821, AK91828, AK91847, AK92111, AK92149, AK92157, AK92170, AK99953, AK99966, AK99984, AK101153, AK131830, AK-L9203, AK-L21170. **Taupiri**

Fig. 10 (opposite). Anatomy of *Phenacohelix tholoides* (Suter). Scale lines = 1mm. A-E. AK154067, Ngahau Bay. F. AK155650, Mahurangi Pt. G. AK154354, Waitononi. H. AK152179, Ngahau Bay. A. Ovotestis. B. Reproductive organs. C. Buccal mass, showing entry of oesophagus. D. Pallial organs, ventral view. E. Posterior portion of foot. F. Undeveloped penis. G. Penis at earlier stage than F. H. Reproductive organs which have developed atypically. For key to abbreviations, see Fig. 1.

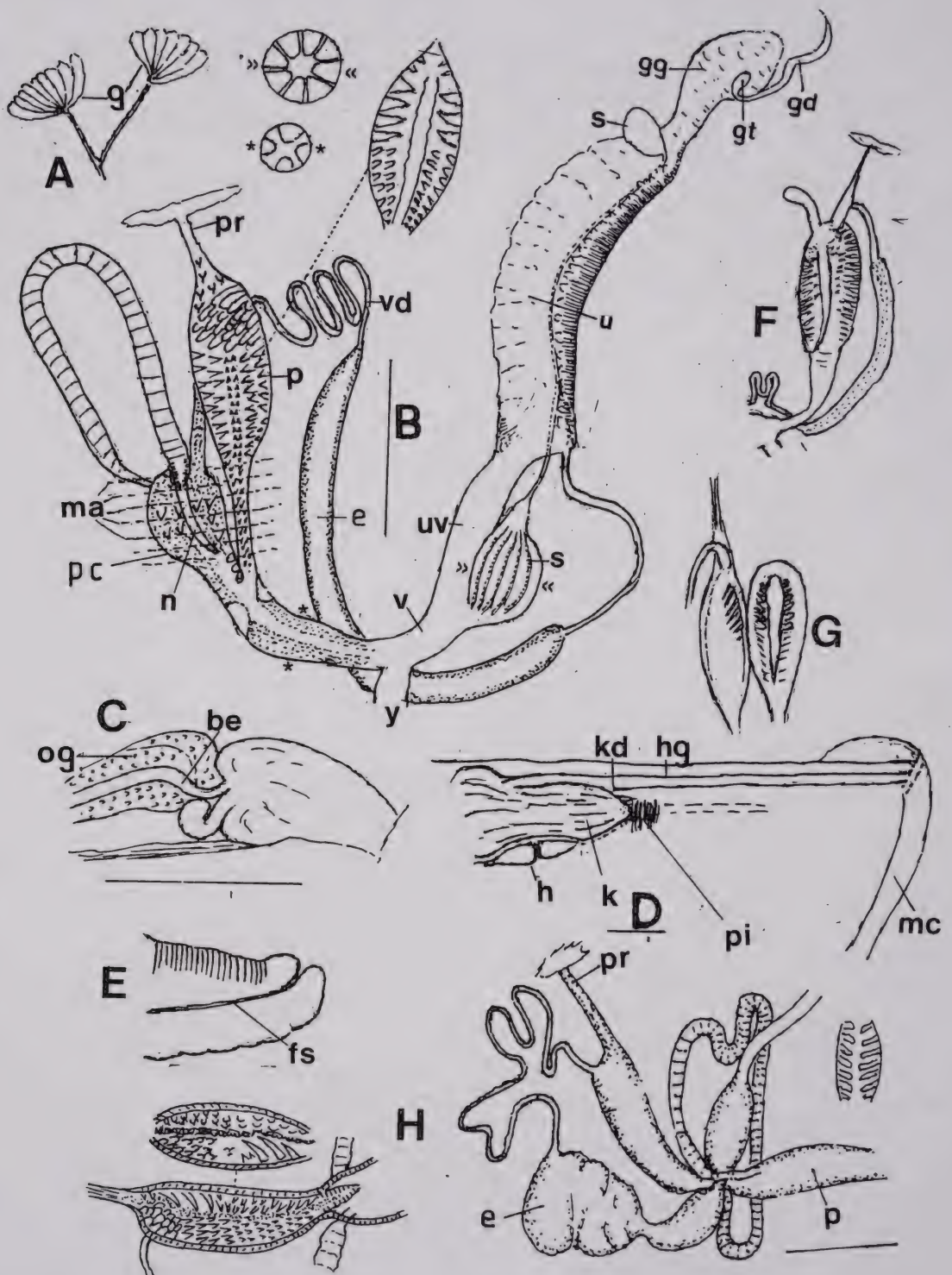


Table 9. Structural features of the shell of *Phenacohelix tholoides* (Suter, 1907) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality	Shell parameters							
	1	2	3	4	5	6	7	8
1 Waitanoni	3.8	3.0	4.1	1.0	1.0	0.2	48	77
2 Mahurangi Pt.	4.1	3.1	4.5	1.1	1.0	0.2	47	80
3 Surville Cliffs	4.8	3.6	5.0	1.3	1.2	0.0	55	149
4 Surville Cliffs	4.6	3.4	4.8	1.1	1.2	0.2	57	144
5 Tapotupotu	3.1	2.3	4.0	1.1	1.6	0.0	45	70
6 Whangaroa	5.1	3.7	5.0	1.0	1.0	0.3	45	97
7 Ngahau Bay	4.5	3.1	4.8	1.0	1.2	0.1	45	83
8 Ngahau Bay	4.5	3.1						
9 Ngahau Bay	4.4	3.0	4.8	1.0	1.1	0.1	49	100
10 Whananaki	4.7	3.4	4.8	1.1	1.2	0.2	47	99

2. AK155650. 3, 4. AK155649. 7. AK152179. 8, 9. AK154067. 10. AK154041. All F.J. Brook. 1. AK154354, P.M. 5. AK155598, J.G. & P.M. 6. AK155371, B.F. Hazelwood.

Is. M02 792469, F.J. Brook & J. McCallum 11/6/88, AK91771. Tokerau Beach O03. A Richardson, AK83215; O04 467939, F.J. Brook 5/11/87, AK95453; O04 467938, F.J. Brook 18/8/94, AK95445. Te Ruatahi Q06 407371, F.J. Brook 7/12/93, AK85548; Q06 404372, F.J. Brook & J.F. Goulstone 17/4/94, AK85065.

RECENT: Te Paki, Herangi M02 799479, F.J. Brook 1/1/94, AK100003; M02 803471 60 m, F.J. Brook 8/12/94, AK-L11995. Te Werahi M02 812478, F.J. Brook 5/5/96, AK151934; M02 812478, F.J. Brook 5/5/96, AK-L20760. Cape Maria van Diemen M02, N. Douglas 26/5/71, AK152057; L. Fitzgerald, AK83213; M02 787474, F.J. Brook 30/9/95, AK-L17788, AK-L17789. Cape Reinga A.W.B. Powell, AK83365. Tapotupotu M02 838511, 7/2/67, AK83214; M02 839511, L. Price 22/7/81, AK153504; M02 851515, D. Hole 7/1/75, AK154111; M02 852515 5 m, J.F. Goulstone 11/5/91, AK-L10450; M02 851517 5 m, J.F. Goulstone 18/11/98, AK155595; M02 840509 40 m, J.F. Goulstone & P.C. Mayhill 16/11/98, AK155598; M02 838512, B.F. Hazelwood & J. Marston 5/6/96, AK-L20763. Pandora M02 908408, J.F. Goulstone 12/5/91, AK96194; M02 891478, J.F. Goulstone 11/5/91, AK-L8940. Kauri Bush M02 895476 260 m, P.C. Mayhill 1/11/97, AK154368; M02 894477 130 m, J.F. Goulstone & P.C. Mayhill 18/11/98, AK155612, AK155614; A.W.B. Powell, 1/1/48, AK83240. Kohuronaki N02 958461, N. Douglas 17/10/74, AK151620; N02 967448 40 m, J.F. Goulstone & P.C. Mayhill 17/11/98, AK155609; N02, N. Douglas 2/6/69, AK-L2192. Spirits Bay N02, N. Gardner 27/12/47, AK83242; N02 989526, D. Hole 2/1/75, AK154091. Waterfall Gully N02, C. Barker 1965, AK83237, AK83241. Maungapiko N02 983534, J.F. Goulstone 11/5/91, AK83210. Waitanoni Valley N02 998525 130 m, P.C. Mayhill 1/11/97, AK154354. Te Hapua Rd. N02 997449 30 m, J.F. Goulstone & P.C. Mayhill 17/11/98, AK155602; N02, N. Douglas 13/5/73, AK83212, 25/5/71, AK154340. Unuwaho N02 274 m, A.W.B. Powell 1/2/32, AK25439. Waihi Stream N02 005527, J.F. Goulstone 10/5/91, AK83209. North Cape Block 30/4/68, AK83239; Mahurangi Pt. N02 102544 20 m, F.J. Brook 11/12/98, AK155650. Surville Cliffs N02 120562 200 m, F.J. Brook 11/12/98, AK155649. Kerr Pt. N02, 1/1/52, AK83216. A.W.B. Powell 23/3/49, AK83238. Karikari Bay O03 463065, N. Douglas 28/5/69, AK152095, AK152096. Whakaangi O04 616944 335 m, L. Price 1/1/60, AK153502. Parauui Scenic Reserve O04 513814 40 m, P.C. Mayhill 1/4/83, AK154854. Whangaroa P04 788826, B.F. Hazelwood 24/5/98, AK155210; P04, C. Cooper 1930, AK26071; P04, A. Hamilton, AK64142. Coppermine Rd. P04 770757 80 m, P.C. Mayhill 1/10/84, AK154697. Te Whau P04 912721; N. Douglas 6/6/69, AK152110. Matauri Bay P04 944841, N. Douglas 17/11/70, AK152130; P04 934843,

B.F. Hazelwood 29/8/98, AK-L21911. **Tauranga Bay Stream** P04 834870, D. Hole 9/1/75, AK154112. **Te Ngaire** P04 912856 80 m, P.C. Mayhill 1/11/88, AK154881; P04 913856, B.F. Hazelwood 24/5/98, L21824, AK-L21904. **St. Pauls Rock Reserve** P04 795832, B.F. Hazelwood 28/8/98, AK155371. **Mangataipo Rd.** O05 592622 40 m, P.C. Mayhill 1/3/96, AK154901. **Bland Bay** Q05 344466 20 m, P.C. Mayhill 1/5/78, AK154926. **Moanarua Is.** Q05 357497, F.J. Brook 13/3/96, AK-L20709. **Moturoa Is.** Q05 104648 10 m, P.C. Mayhill 1/1/90, AK154856. **Mimiwhangata** Q06 397367, F.J. Brook & J.F. Goulstone 10/12/93, AK83211; Q06 375370, F.J. Brook & J.F. Goulstone 22/4/94, AK85190; Q06 399398, F.J. Brook & J.F. Goulstone 18/4/94, AK85338, AK85201, AK85504. **Ngahau Bay** Q06 373392, F.J. Brook 22/6/94, AK152179, AK154067, F.J. Brook & J.F. Goulstone 19/9/94, AK154067, F.J. Brook & J.G. 19/4/94, AK85574. **Te Ruatahi Is.** Q06 408371, F.J. Brook & J.F. Goulstone 7/12/93, AK85597. **Helena Bay** Q06 343398, F.J. Brook 18/6/94, AK89191; Q06 349393, F.J. Brook 14/5/94, AK89280; Q06 356395, F.J. Brook 15/5/94, AK89371, Q06 349393, F.J. Brook 14/5/94, AK-L10354. **Whananaki** Q06 444309, F.J. Brook 20/9/94, AK154041.

DISTRIBUTION AND HABITAT

Phenacohelix tholoides ranges from Te Paki in the Far North to Whananaki, just north of Whangarei, with a mainly eastern distribution. Although *P. tholoides* is found at inland sites, it is more prominent near the sea where it may be found in a wide range of litter types, such as that of pohutukawa (*Metrosideros excelsa*), flax, *Pseudopanax* sp., and mahoe (*Melicytus ramiflorus*). It also lives under rotting logs and in fallen nikau fronds.

Phenacohelix ziczag (Gould, 1846), new combination

Figs 11, 12

DESCRIPTION

External Morphology

Foot white, its margin crenellated and surmounted by two pedal grooves. Dorsal surface of foot grey, crinkled.

Reproductive Anatomy

Ovotestis comprises two clumps of finger-like alveoli (0.6 mm wide). Hermaphrodite duct initially slender but gradually becomes distended as medial seminal vesicle, then abruptly narrows to terminate in carrefour embedded within the albumen gland. Talon not observed. Albumen gland (up to 4 mm x 2 mm) ovoid. Spermoduct 5 mm long, narrow where it joins albumen gland (0.3 mm) but expands three-fold or more to form ovoid organ dominated by oviductal glands but with prominent band of prostatic alveoli visible along its entire length. Free oviduct variable in width (0.2–0.4 mm), 1.6 mm long. Spermathecal duct with a prominent, bulbous swelling (1.5 mm long) immediately above its opening to the vagina, with narrow lumen, then abruptly forming a slender duct terminating in an oval sac (1.1 mm long) resting against the albumen gland. Vagina generally long (1.4 mm), tubular, uniformly wide throughout (0.3 mm). Vas deferens slender throughout, terminating in apex of the penis adjacent to the penial retractor muscle. Epiphallus not observed. Retractor muscle rising from diaphragm close to the base of the kidney. Penis (3.8 mm long) somewhat variable in shape but generally comprising three proximal chambers and a distal tubular connection to the atrium. The most proximal chamber is elongate (1.4 mm long), equipped internally with small, spinate papillae in sexually immature animals, these reducing in mature animals and lumen becoming dominated by longitudinal folds. The second and third proximal chambers, each increasingly larger, tend to be bulbous, equipped internally with both small, and very large, spinate papillae in immature

animals, and predominately with ridges and folds in mature animals. The third chamber bears a prominent lateral, sacculate caecum. In immature animals the caecum is equipped with one or two solid darts, anchored on the farthest wall and projecting towards the penial lumen, and two tubular glands evidently opening to the penis, in addition to numerous minute papillae. In older specimens the darts are frequently absent and the glands often somewhat degenerate.

Other Anatomy

Pallial cavity 10 mm long, with little pigmentation on upper membrane. Mantle collar 3.5 mm wide. Kidney (4.2 mm long) has strong pericardial lobe with heart (1.5 mm long) recessed in outer wall, and small, rounded rectal lobe. Ureter skirts along anterior face of the pericardial lobe from its apex to junction with renal lobe, then turns forward adjacent to hindgut to open through respiratory pore slightly behind anus. Reflexed arms of ureter well separated. Oesophagus, with flanking salivary gland ducts, enters dorsal-posterior aspect of the buccal mass. Salivary glands occupy considerable space surrounding oesophagus immediately in rear of buccal mass.

REMARKS

Six specimens of *Phenacohelix ziczag* were dissected (Table 10). I have figured the considerable progression of characters in the penis lumen between young and old specimens of *P. ziczag*. The size of the shell in this species, as is the case in *P. tholoides*, is not a good indicator of stage in sexual development. The darts and spinate papillae of the young specimens are replicas of those found in *P. tholoides* and *P. giveni*, but in the present species the darts are evidently not permanent fixtures and the papillae tend to be replaced with ridges and channels in older specimens. The oldest specimen dissected (ex Waipoua Forest) had a small dart, suggesting that darts lost during sexual activity are replaced. This individual also had a yellow-orange spermatophore lodged in the base of the spermathecal duct, indicating that the epiphallus is present, albeit not sufficiently differentiated from the vas deferens to be apparent in dissections. The penial caecum is equipped with paired, tubular glands. In one dissection, these glands were considerably reduced, with the caecum containing indeterminate solid matter. This suggests considerable dynamism in the condition of the secretory activity.

DISTRIBUTION AND HABITAT

Phenacohelix ziczag occupies the northern part of the North Island except the Far North at Te Pahi. It lives in all kinds of litter, and can tolerate coastal situations with much sea spray. I have found it occasionally with *P. giveni* in nikau fronds or under logs or bark. It also tucks into rock or wood crevices.

Fig. 11 (opposite). Anatomy of *Phenacohelix ziczag* n. comb. Scale lines = 0.5 mm (B) or 1 mm (A, C-I). A-D. AK-L21719, Waipoua Forest. E. AK155160, Hakarimata Ra. F. AK155158, Lake Tarawera. G. AK154570, Albany. H. AK154568, Waipipi Sc. Res. I. AK154570, Albany. A. Reproductive organs. B. Ovotestis. C. Posterior portion of foot. D. Pallial organs, ventral view. E. Younger specimen than B. F. Large specimen without tubes or needles in penial epiphallus. G. Young specimen with penis lumen just developing. H. Penis lumen from a fairly well developed shell just prior to penial epiphallus developing. I. Reproductive organs from shell slightly larger than that of H, with developing epiphallus but containing only one large needle. For key to abbreviations, see Fig. 1.

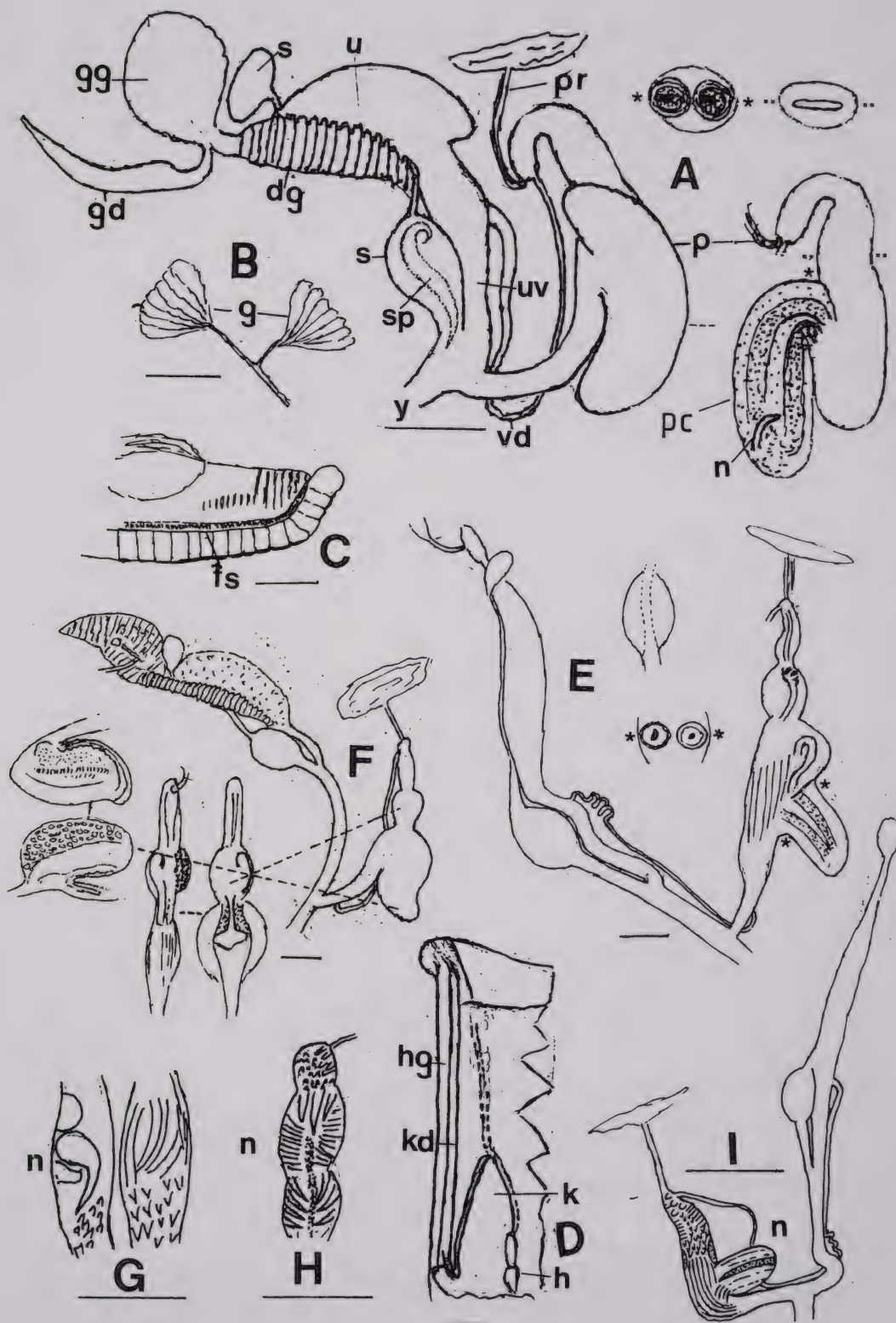


Table 10. Structural features of the shell of *Phenacohelix ziczag* (Gould, 1846) based on measurements taken from representative shells of adults from selected localities. Shell parameters: 1 = width; 2 = height; 3 = whorls; 4 = protoconch width; 5 = last whorl width; 6 = umbilicus width; 7 = number of ribs on 1st teleconch whorl; 8 = number of ribs on last teleconch whorl.

Locality	Shell parameters							
	1	2	3	4	5	6	7	8
1 Waipoua Forest	9.5	5.5	5.8	1.3	2.7	2.0	49	81
2 Albany	7.7	4.6	4.8	1.3	2.2	1.2	30	64
3 Albany	7.5	4.5	4.5	1.3	2.2	1.2	30	65
4 Waipipi Sc. Res.	6.9	4.1	4.5	1.3	2.4	1.3	26	54
5 Hakarimata Ra.	8.9	5.3	5.2	1.4	3.0	1.1	42	80
5 Hakarimata Ra.	8.4	5.6	5.0	1.3	2.9	1.1	36	85

1. AK-L21719, O06 623165 G.M. Barker 1/7/91. 2, 3. AK154570, R10 592974 100 m, J.F. Goulstone 17/10/97. 4. AK154568, R12 580412, J.F. Goulstone 30/12/97. 5. AK155160, 38°50'S 175°07.5'E, G.M. Barker 29/12/91. 6. AK155158, 38°11'S 176°26'E, G.M. Barker 1/1/80.

DISCUSSION

From an anatomical point of view *P. pilula* and *P. ponsonbyi* are very similar, both having the tubular penial caecum. *P. giveni* and *P. tholoides* have a more complex penial caecum containing a substantial section with spinate papillae and a large hollow dart connected to a tubular gland. The structure is basically similar in *P. ziczag*, except that the dart and glands are primarily paired and the gland is housed inside the caecum rather than external. These five species also have similar shell features. Having similar shell features to all the foregoing, but with a poorly developed penial caeca are *P. hakarimata* n. sp., *P. perplexa*, *P. aurea* n. sp., *P. brooki* n. sp. and *P. mahlfeldi* n. sp. In *P. lucetta* the penial caecum is evidently strongly reduced. Thus the dissected species form a gradient from the condition in which the male genitalia are equipped with dart(s) and associated gland(s) through to that in which these structures are vestigial. In the absence of a clear 'break point' in this gradient, I have retained all these dissected species within the genus *Phenacohelix*. This is the first observation of complex, dart-bearing stimulatory organs in the family Charopidae.

Live *Phenacohelix* are often plentiful, but populations are frequently dominated by immature specimens and it is often difficult to find specimens in the upper quartile of the shell size range for the species. Further, shell size or shell whorl number is often a poor indicator of the sexual maturity of the animal. That is, a shell of mature appearance may contain an animal with underdeveloped genitalia. It would be desirable to examine a series to ascertain the extent of variation among individuals and the extent to which reproductive features change with age.

Acknowledgements: I am very much indebted to those people who have collected live snails for me, namely Gary M. Barker, Fred J. Brook, Bruce F. Hazelwood and Pauline C. Mayhill. Mrs Mayhill has also donated to the Auckland Museum *Phenacohelix* shells of all species from many localities. Frank M. Climo and Karin Mahlfeld of Wellington have been helpful in many ways. The staff of the Auckland Museum marine section (Ramola Prasad, Glenys Stace and Maree Johnson) have been supportive.

Fig. 12 (opposite). Distribution maps for the species of *Phenacohelix* discussed in this paper, compiled from records of specimens in the Auckland Museum collection.